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# MONOGRAPH OF THE NEOTROPICAL SPECIES OF *ASPLENIUM* SECT. *HYMENASPLENIUM* (ASPLENIACEAE)[1]

*Noriaki Murakami*[2] *and*
*Robbin C. Moran*[3]

## Abstract

*Asplenium* sect. *Hymenasplenium* is one of the best defined groups of *Asplenium*, being characterized by creeping rhizomes, dorsiventrally symmetrical steles, swollen petiole bases, unique rachis-costae structure, and chromosome base numbers of $x = 38$ or 39. In the Neotropics, the section has ten species and three hybrids. The species are *A. delitescens*, *A. hoffmannii*, *A. laetum*, *A. obtusifolium*, *A. ortegae*, *A. purpurascens*, *A. repandulum*, *A. riparium*, *A. triquetrum*, and *A. volubile*. The hybrids are *A.* ×*papyraceum* (of unknown parentage), *A. delitescens* × *A. laetum*, and *A.* ×*incisoserratum* (= *A. hoffmannii* × *A. laetum*). All the aforementioned species and hybrids are endemic to the Neotropics. Central America and the Andes harbor the most species and endemics. A cladistic analysis was not done because the neotropical species of the section apparently do not form a monophyletic group separate from the paleotropical ones.

Section *Hymenasplenium* is one of the best defined groups within *Asplenium*, distinguished by the following synapomorphies: creeping rhizomes, dorsiventrally symmetrical steles, swollen petiole bases, unique rachis-costae structure and chromosome base numbers of $x = 38$ or 39. All other *Asplenium* species have erect or ascending rhizomes, radially symmetrical steles, nonswollen petiole bases, and $n = 36$ or multiples thereof (rare exceptions differ in only one of these characteristics).

*Hymenasplenium* was first described by Hayata

[1] We thank the curators of the following herbaria for making loans available: A, AAU, B, BM, BR, COL, CR, F, G, GH, K, L, M, MICH, NY, PORT, QCNE, S, U, UC, Z. We also thank the following botanists who helped one or both of us with fieldwork in Latin America: George Anger, Gerardo Aymard, Mireya Correa, Lisa and Larry Dorr, Michael Grayum, Hiroshi Kidono, María Morrello, David Neill, Benjamin Øllgaard, Francisco Ortega, and Pablo Sánchez. We also thank the Smithsonian Tropical Research Institute for the use of its Fortuna Dam facilities when we worked in Panama, and UNELLEZ in Guanare, Venezuela, for the use of its facilities. The research for this paper was done while the first author worked at the Missouri Botanical Garden supported by a grant from The Japanese Society for the Promotion of Science. He thanks Peter H. Raven, who served as his official host. Finally, we thank our wives, Misaki Murakami, who did the illustrations, and Cirri K. R. Moran, who helped with the computer-related aspects of the research.

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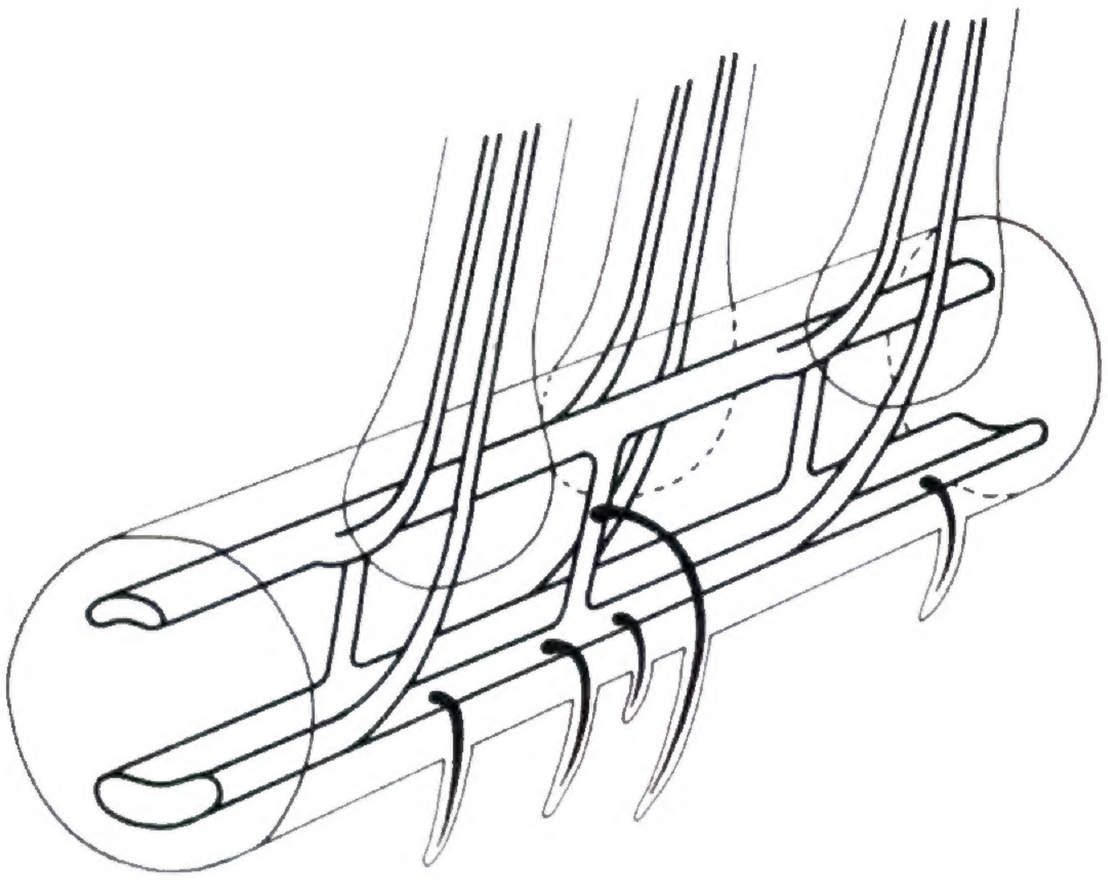


FIGURE 1. Creeping rhizome, dorsiventral stele, and swollen leaf bases—characteristics of *Asplenium* sect. *Hymenasplenium*.

(1927) as a monotypic genus based on *A. unilaterale* Lam. and distinguished entirely by the stelar structure of the long-creeping rhizome (Fig. 1). Hayata was greatly influenced by stelar structure and described several genera based solely upon this character (e.g., *Diploblechnum*, *Monachosorella*, *Boniniella*, *Pentarhizidium*, and *Hymenasplenium*). Iwatsuki (1975) revised the species of *Hymenasplenium*, which were then thought to occur primarily in the Old World, and reduced the genus to a section of *Asplenium*. This ranking has been followed by nearly all pteridologists, including us.

The present monograph treats 10 neotropical species that clearly belong to section *Hymenasplenium* alongside the Old World species. (The Old World species of the section are *A. apogamum* Murakami & Hatanaka, *A. cardiophyllum* (Hance) Baker, *A. cataractarum* Rosenstock, *A. cheilosorum* Kunze, *A. excisum* C. Presl, *A. hondoense* Murakami & Hatanaka, *A. obliquissimum* (Hayata) Sugimoto & Kurata, *A. obscurum* Blume, *A. subnormale* Copel., and *A. unilaterale* Lam.) We have not done a cladistic study of the neotropical species because they are not a monophyletic group distinct from the paleotropical species. The first author plans to do a cladistic study of all the species in the section worldwide using evidence from morphology, anatomy, chloroplast DNA, and nuclear gene sequencing of the small subunit of ribulose-bis phosphate carboxylase. The only difference we have seen between the Old and New World species is that the New World ones have proliferous roots, whereas the Old World ones do not. Proliferous roots do not correlate with any other character (besides geography) and therefore cannot be used to define a natural group.

Previous workers, studying only the Old World species of section *Hymenasplenium*, have surveyed anatomy (Iwatsuki & Kato, 1975; Misuta et al., 1980), reproductive patterns and morphological variation (Murakami & Iwatsuki, 1983), phytochemistry and chemotaxonomy (Murakami & Hatanaka, 1983, 1985, 1988a; Murakami et al., 1985), ecology and morphological variation (Kato & Iwatsuki, 1985, 1986), genetic diversity (Watano & Iwatsuki, 1988), taxonomy (Murakami & Hatanaka, 1988b), and chromosome numbers (Mitui et al., 1989).

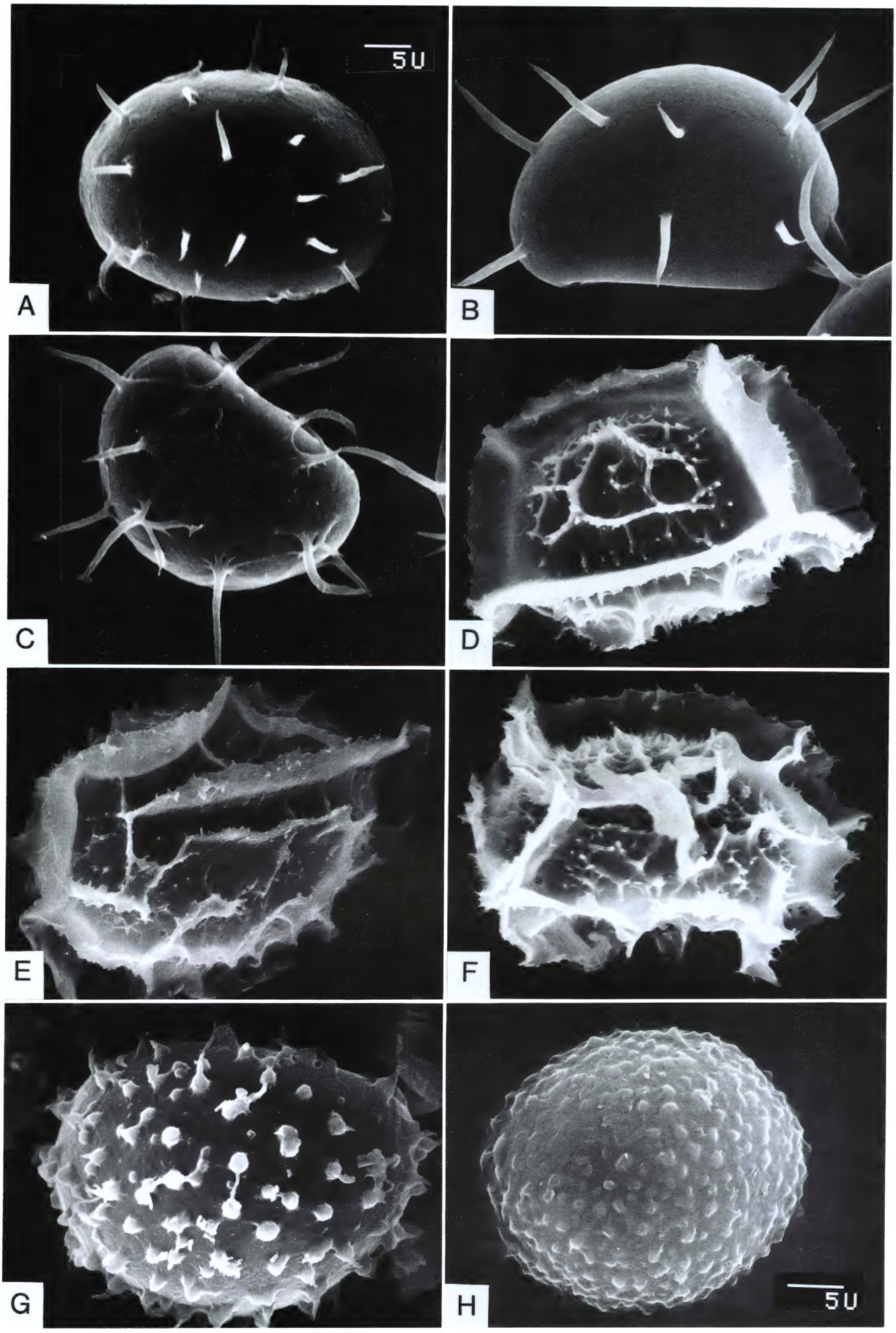
The New World species are much more poorly studied. For a long time, workers in the Old World thought that the only New World species that belonged to section *Hymenasplenium* was *A. obtusifolium*. Smith (1976) was the first to point out that the New World species *A. delitescens*, *A. melanopus* (= *A. purpurascens*), *A. laetum*, *A. hoffmannii*, and *A. repandulum* also belonged to the section. He did not, however, study the group in detail.

## SPORES

We examined the spores of all the neotropical species of section *Hymenasplenium* and found that perispore morphology was useful in defining two groups. The first group has five species, which we informally refer to as the "*repandulum* group." It comprises *A. obtusifolium*, *A. repandulum*, *A. riparium*, *A. triquetrum*, and *A. volubile*. All have spiny spores (Fig. 2A–C) or, in the case of *A. obtusifolium*, papillate spores (Fig. 2G, H). The second group comprises the rest of the neotropical species, which all have cristate spores (Fig. 2D–F). The eight paleotropical species of section *Hymenasplenium* examined by Kato et al. (1990)

→

FIGURE 2. The spores of various neotropical species of *Asplenium*, sect. *Hymenasplenium*.—A. *A. riparium*, Mexico, *Copeland 15940* (MICH).—B. *A. volubile*, Colombia, *Forero et al. 7237* (F).—C. *A. repandulum*, Ecuador, *van der Werff 660* (GH).—D. *A. hoffmannii*, Panama, *Johnston 258* (GH).—E. *A. ortegae*, *Steyermark et al. 127134* (UC).—F. *A. delitescens*, Brazil, *Sperling 6035* (UC).—G. *A. obtusifolium*, race with 32 spores per sporangium, Panama, *Antonio 3530* (MO).—H. *A. obtusifolium*, race with 64 spores per sporangium, Venezuela, *Steyermark et al. 121451* (UC).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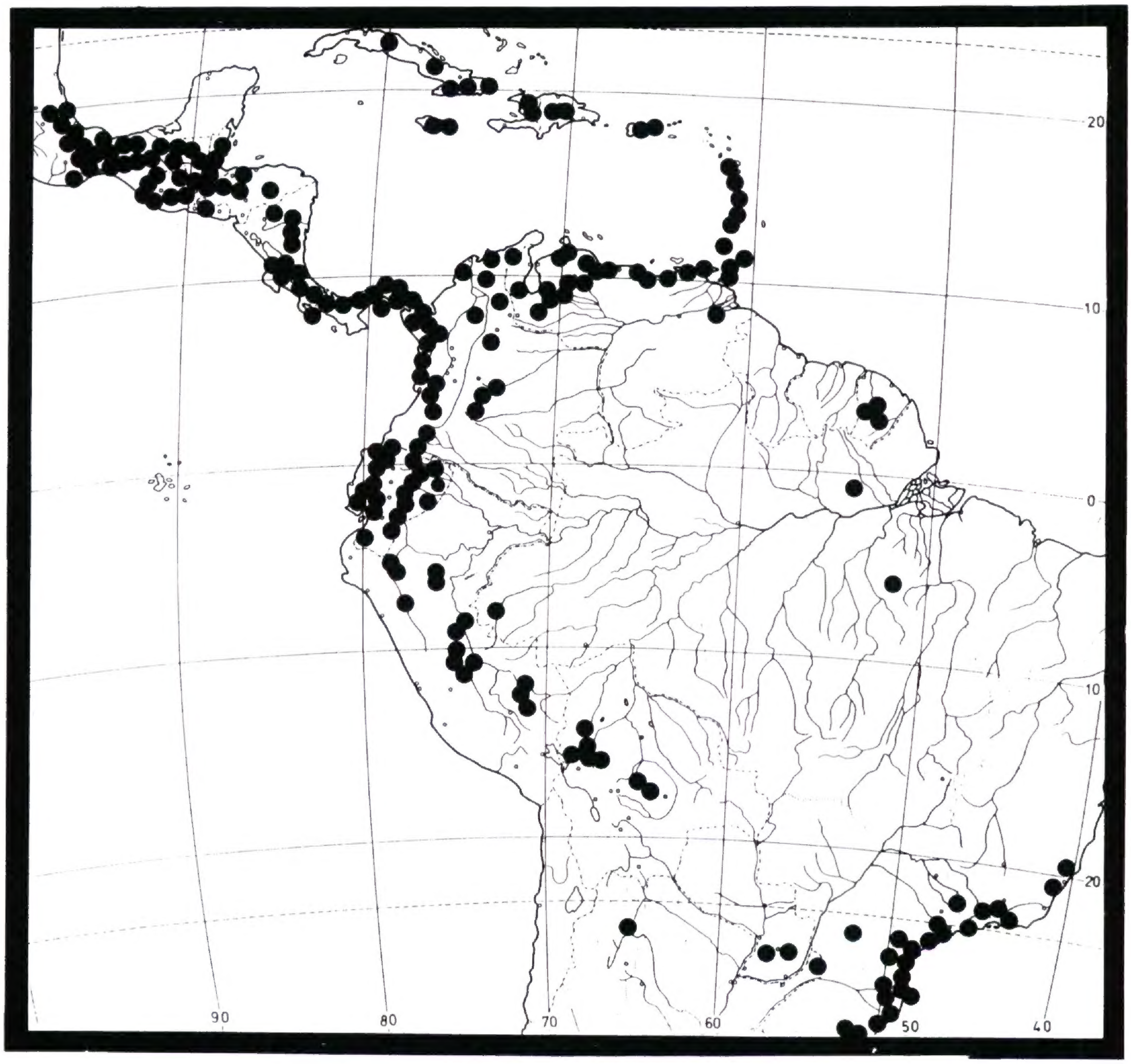



MAP 1. The distribution of *Asplenium* sect. *Hymenasplenium* in the New World.

had cristate spores and would therefore belong to this second group. Because most species of *Asplenium* outside of section *Hymenasplenium* have cristate spores (Tryon & Lugardon, 1991), the spiny and papillate character states should be considered apomorphic.

## GEOGRAPHY

The neotropical species of section *Hymenasplenium* are all endemic to the Neotropics. They range from southern Mexico to Panama, the Antilles, and South America from Venezuela to southeastern Brazil, forming a wide arc around most of Amazonian Brazil (Map 1).

The Andes from Venezuela to Bolivia harbor the most species (8) and this is the only region with endemics (i.e., *Asplenium ortegae*, *A. repandulum*, *A. volubile*). Costa Rica and Panama are also species-rich, containing six species. The Antilles and extreme western Amazonian Brazil both have two species, and the Guianas, southeastern Brazil, and Paraguay all have one species. The Serra do Mar region of southeastern Brazil, which is a center of species richness and endemism for ferns (Tryon, 1972), has played a minor role in the diversification of the section. Only one species (*A. triquetrum*) occurs there and it is nearly endemic (Map 9).

*Asplenium obtusifolium* is notable for its nearly circum-Caribbean distribution (Map 5) and its correlation with geography of the 32- and 64-spored races.

## PRINCIPAL COMPONENTS ANALYSIS

Our recognition of 10 neotropical species of *Asplenium* sect. *Hymenasplenium* is based primarily upon qualitative characters as shown in the key. In order to check the validity of our species circumscriptions, we decided to do a Principal Com-

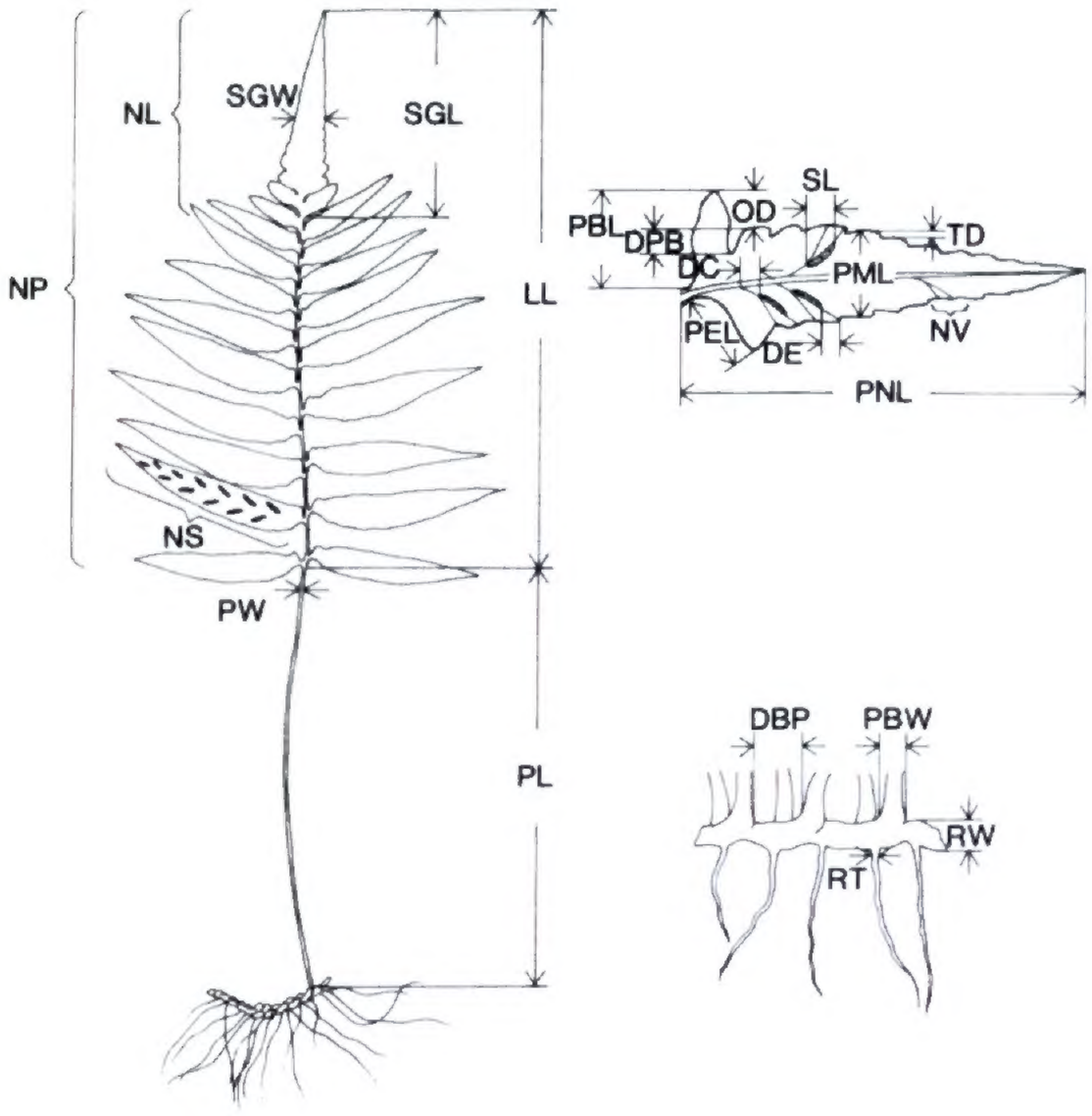



FIGURE 3. Parts of the plants measured for the Principal Components Analyses (Figs. 4, 5). Lamina length (LL), petiole length (PL), petiole width (PW), number of pinna pairs (NP), pinna length (PNL), pinna base length (PBL), pinna width at middle (PML), pinna excised portion length (PEL), number of veins (NV), depth at pinna base (DPB), auricle length (OD), serration depth at tip (TD), number of sori (NS), sorus length (SL), distance to sorus from edge of pinna (DE), distance from costa (DC), segment length (SGL), segment width (SGW), number of lobes (NL), rhizome width (RW), petiole base width (PBW), distance between two petioles (DBP), root width (RT).

ponents Analysis (PCA) of certain quantitative characters (Fig. 3) measured on herbarium specimens throughout the range of each species. We separated the species into two groups according to their separation in the first couplet of the key. The first group, which is identified under lead 1b in the key, contained *A. hoffmannii*, *A. laetum*, *A. delitescens*, *A. purpurascens*, and *A. ortegae*. The second group, which we believe to comprise a closely related group of species and which is identified under lead 1a of the key, contained *A. obtusifolium*, *A. repandulum*, *A. riparium*, *A. volubile*, and *A. triquetrum*. Then, we did a PCA on each group using computer program NTSYS version 1.40 (Rohlf, 1988). The data set for each herbarium specimen was projected on three principal component axes for the first group (Fig. 4) and two axes for the second group (Fig. 5; the third axis accounted for little variation in the second group). Tables 1 and 2 show the Eigen values and Eigen vectors of the Principal Components.

The result for the first group was that all species were separated from each other (Fig. 4). This result supports our circumscriptions of the species.

The result for the second group was not as clear (Fig. 5). Although *A. obtusifolium*, *A. riparium*, and *A. volubile* were separated from each other, *A. repandulum* completely overlapped *A. triquetrum* and *A. volubile*. *Asplenium repandulum*,

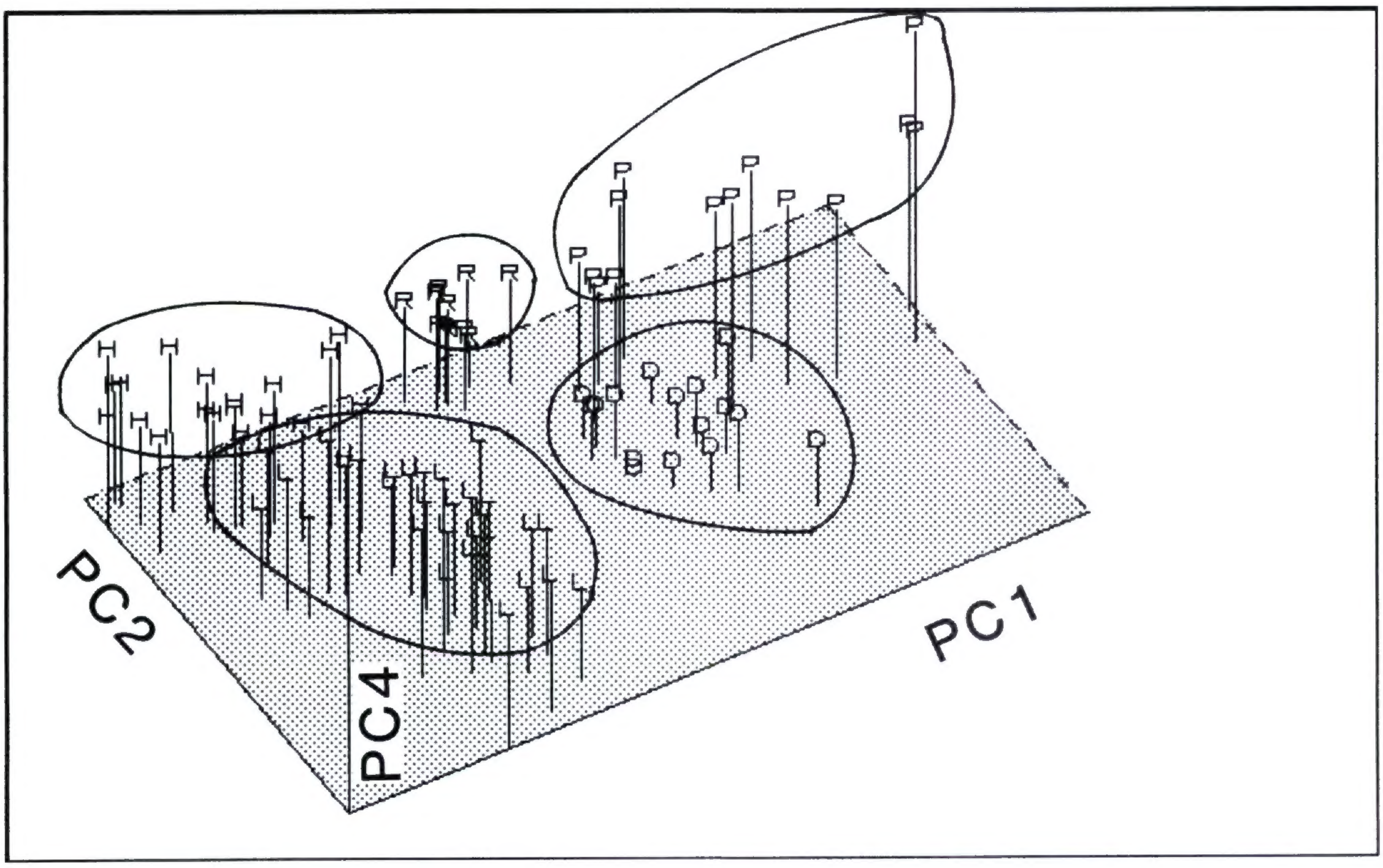



FIGURE 4. Principal Components Analysis of 23 characters of *A. delitescens* (D), *A. hoffmannii* (H), *A. laetum* (L), *A. ortegae* (R), and *A. purpurascens* (P). The three Principal Component axes account for 62% of the measured variation.

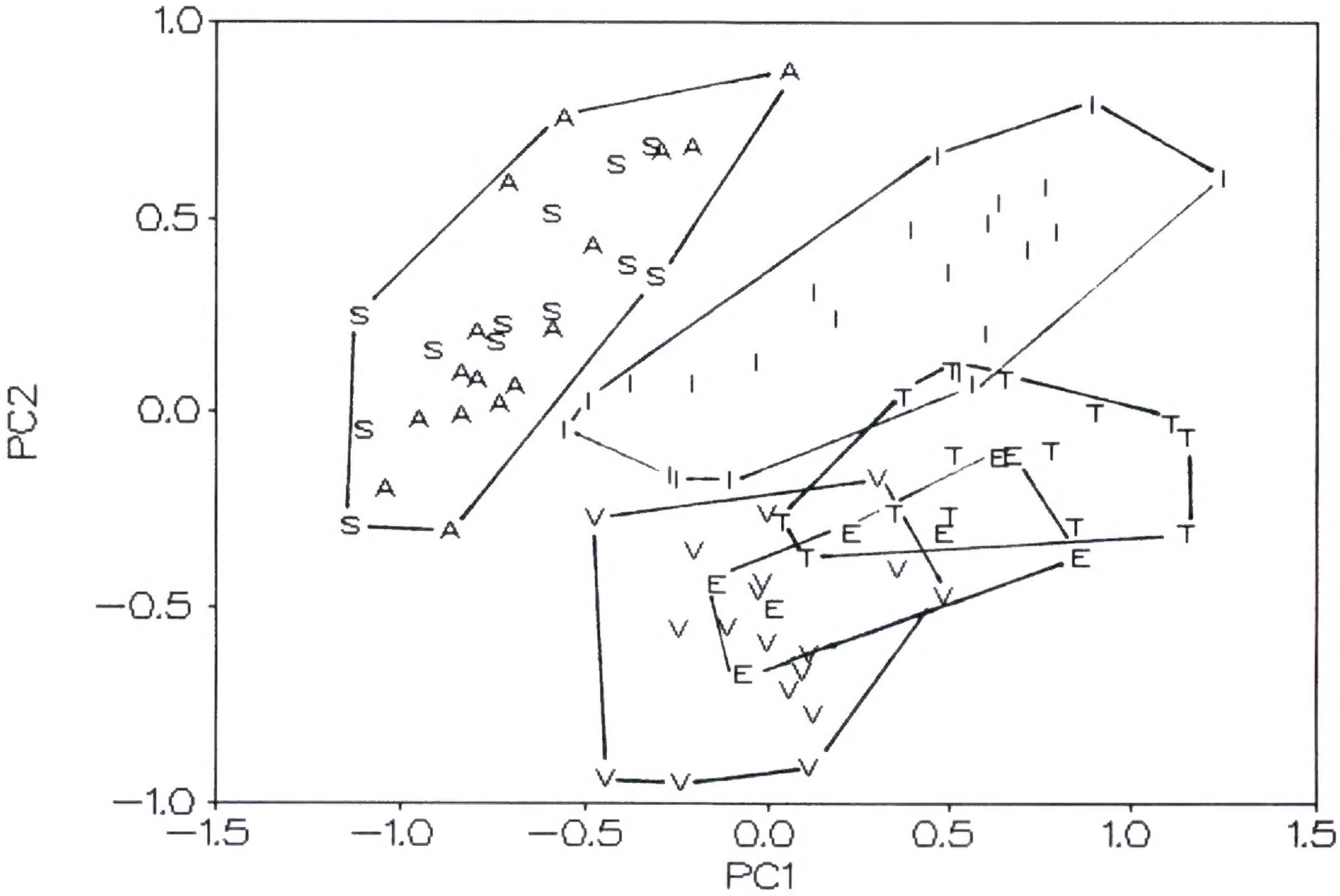



FIGURE 5. Principal Components Analysis of 20 characters of *A. obtusifolium* (A, 32-spored race; S, 64-spored race), *A. repandulum* (E), *A. riparium* (I), *A. volubile* (V), and *A. triquetrum* (T). The two Principal Component axes account for 54% of the measured variation.

however, can be distinguished from *A. triquetrum* by petiole length relative to the lamina, habitat, and range (see key, couplet 4), and from *A. volubile* by the carinate rachis and rachidial wings parallel to the plane of the lamina. These characteristics were not included in the measurements used for the PCA. Another result was that the two spore-races of *A. obtusifolium* could not be separated by the morphological characteristics measured (Fig. 5).

## Relationship to Other Groups of *Asplenium*

We are not sure what group of species within *Asplenium* is most closely related to section *Hymenasplenium*. Several species of *Asplenium* (*A. abscissum* Willd., *A. argentinum* Hieron., *A. hostmannii* Hieron., and *A. otites* Link) greatly resemble certain species in section *Hymenasplenium* in leaf form. Consequently, they are often misidentified as a species in section *Hymenasplenium*, especially *A. laetum* (which see for comparison). These species, which can be immediately distinguished from section *Hymenasplenium* by their erect rhizomes and rachis-costa architecture, may be the closest group in *Asplenium* related to section *Hymenasplenium*. This suggestion is based only on similarities in leaf form and is therefore tentative.

## Taxonomic Treatment

**Asplenium** sect. **Hymenasplenium** (Hayata) Iwatsuki, Acta Phytotax. Geobot. 27: 44. 1975. Basionym: *Hymenasplenium* Hayata, Bot. Mag. (Tokyo) 41: 712. 1927. TYPE: *Asplenium unilaterale* Lam.

Plants terrestrial, epipetric, or epiphytic; rhizome creeping, green to blackish, with two rows of alternately arranged petioles on the dorsal surface, scaly near the apex; rhizome stele dorsiventral, composed of two unequal meristeles connected by lateral strands, the ventral meristele wider and the dorsal one narrower, bearing roots from either the ventral, dorsal, or connecting meristeles; petiole terete, scaly at base, glabrous distally, greenish to atropurpureous, the base swollen and often persisting after the leaf has fallen and decayed; lamina usually 1-pinnate or (in *A. cardiophyllum*) simple and cordate; rachis not or very shallowly grooved, with or without perpendicular or flat green wings, lacking buds; costae bordered by a flange of green

TABLE 1. The Eigen vector values for each PC in the analyses of *A. delitescens*, *A. hoffmannii*, *A. laetum*, *A. ortegae*, and *A. purpurascens* (Fig. 4).

| Character (Fig. 3) | Principal component | | | |
|---|---|---|---|---|
| | 1 | 2 | 3 | 4 |
| LL | 0.579 | −0.699 | 0.200 | 0.043 |
| PL | 0.896 | −0.233 | 0.086 | 0.064 |
| PW | 0.833 | −0.151 | 0.110 | −0.055 |
| NP | −0.112 | −0.811 | 0.388 | 0.172 |
| PNL | 0.936 | 0.032 | −0.045 | −0.143 |
| PBL | 0.579 | −0.531 | −0.393 | 0.072 |
| PML | 0.912 | 0.098 | −0.237 | −0.030 |
| PEL | −0.044 | −0.720 | −0.497 | −0.163 |
| NV | 0.796 | 0.432 | 0.170 | 0.077 |
| DPB | 0.263 | 0.165 | −0.370 | 0.696 |
| OD | −0.157 | −0.304 | 0.395 | 0.157 |
| TD | −0.245 | 0.306 | −0.617 | 0.128 |
| NS | 0.737 | 0.093 | 0.018 | 0.428 |
| SL | 0.667 | −0.028 | −0.098 | −0.129 |
| DE | 0.272 | 0.130 | −0.225 | −0.469 |
| DC | 0.058 | −0.542 | −0.614 | −0.113 |
| SGL | 0.732 | −0.092 | −0.101 | −0.336 |
| SGW | 0.838 | 0.241 | −0.096 | −0.018 |
| NL | 0.757 | 0.403 | 0.074 | −0.176 |
| RW | 0.483 | −0.435 | 0.274 | 0.054 |
| PBW | 0.752 | −0.159 | 0.051 | 0.161 |
| DBP | 0.614 | 0.172 | −0.075 | 0.481 |
| RT | 0.782 | 0.223 | 0.279 | −0.303 |

TABLE 2. The Eigen vector values for each principal component in the analyses of *A. obtusifolium*, *A. repandulum*, *A. riparium*, *A. volubile*, and *A. triquetrum* (Fig. 5).

| Character (Fig. 3) | Principal component | |
|---|---|---|
| | 1 | 2 |
| LL | 0.866 | −0.343 |
| PL | 0.721 | 0.337 |
| PW | 0.646 | 0.218 |
| NP | 0.696 | −0.561 |
| PNL | 0.887 | 0.089 |
| PBL | 0.649 | 0.291 |
| PML | 0.659 | 0.452 |
| PEL | 0.010 | 0.722 |
| DPB | −0.602 | 0.491 |
| OD | 0.511 | −0.355 |
| TD | −0.392 | 0.560 |
| NS | 0.798 | −0.214 |
| SL | 0.599 | 0.309 |
| DE | 0.476 | 0.413 |
| DC | 0.024 | 0.523 |
| SGL | 0.489 | 0.363 |
| SGW | 0.314 | 0.590 |
| RW | 0.645 | 0.089 |
| PBW | 0.770 | −0.041 |
| DBP | 0.264 | −0.702 |

tissue that is decurrent on the adaxial surface of the rachis; decurrent margins of the pinnae not thickened; veins free or (in *A. cardiophyllum*) anastomosing; spores bilateral, ellipsoid to subglobose, the perispore commonly cristate, but occasionally spiny or papillose; $x = 38$ or 39.

**1. Asplenium delitescens** (Maxon) L. D. Gómez, Brenesia 8: 52. 1976. *Diplazium delitescens* Maxon, Contr. U.S. Natl. Herb. 10: 497, t. 56, fig. 1. 1908. TYPE: Cuba. Oriente: vic. of San Luis, 18 Feb. 1902, *Pollard & Palmer 348* (holotype, US; isotypes, F, MO). Figure 6A; Map 2.

Plants terrestrial; roots 1–1.5 mm wide; rhizome 3.5–7 mm wide, nearly naked; scales 2–2.5 mm × 0.25–0.35 mm, black-brown, narrowly lanceolate, toothed; petiole bases 2.8–4.5 mm wide, swollen, 1–2 mm distant from each other on the same row; petiole 15–25 × 0.15–0.2 cm, ca. ½ the

KEY TO THE NEOTROPICAL SPECIES OF *ASPLENIUM* SECT. *HYMENASPLENIUM*

1a. Leaf apex conform, subconform, or hastate; spores spiny or papillose; rhizome greenish when living (sometimes turning blackish upon drying).
  2a. Pinna apices obtuse or rarely acute; pinna pairs 3–10, usually with a free basal acroscopic lobe; spores papillose; plants rheophytic, usually under or near waterfalls; Costa Rica, Panama, Colombia, Venezuela, Antilles ..... 4. *A. obtusifolium* L.
  2b. Pinna apices acute or rarely obtuse; pinna pairs 8–18, usually without a free basal acroscopic lobe; spores spiny; plants epiphytic or epilithic and (usually) on rocks along streams.
    3a. Rachis strongly carinate abaxially, triangular in cross section, with adaxial green wings in the same plane as the lamina (these wings are difficult to distinguish in dried material); Ecuador, Peru, Bolivia, Paraguay, southern Brazil.
      4a. Plants epilithic; petiole ca. ½ as long as the lamina length; Bolivia, Paraguay, southern Brazil ..... 9. *A. triquetrum* Murakami & R. C. Moran
      4b. Plants epiphytic; petiole ¼–½ as long as the lamina; Amazonian Ecuador and Peru ..... 7. *A. repandulum* Kunze
    3b. Rachis rounded abaxially, terete or semi-terete in cross section, with adaxial green wings perpen-

dicular to the plane of the lamina (the wings difficult to see in dried specimens); southern Mexico to western Venezuela and Ecuador.

5a. Petioles ¼–½ as long as the lamina; plants twining around small trees or saplings; rhizome internodes 1–2.5 cm long; Costa Rica, Panama, western Colombia, western Ecuador ..... 10. *A. volubile* Murakami & R. C. Moran

5b. Petioles ½ to equaling the lamina; plants usually on boulders along streams; rhizome internodes 0.2–0.6 cm long; Mexico to western Venezuela and Ecuador ..... 8. *A. riparium* Liebm.

1b. Leaf apex nonconform, pinnatifid; spores cristate; rhizome brown or blackish when living.

6a. Free pinna pairs 2–6(–8); rachis green; Mexico to Panama, Trinidad, Venezuela, Colombia ..... 2. *A. hoffmannii* Hieron.

6b. Free pinna pairs 6–25; rachis atropurpureous to castaneous.

7a. Veins (in the middle of the pinnae) 2–4-forked; rachis grooved, with an adaxial green wing perpendicular to the plane of the lamina; western Venezuela, and Ecuador and Peru on the eastern side of the Andes ..... 5. *A. ortegae* Murakami & R. C. Moran

7b. Veins (in the middle of the pinnae) 1–2-forked; rachis grooved but without adaxial green wings.

8a. Pinnae pinnatifid throughout their length, usually lobed ¼–½ to the costae; Ecuador ..... 6. *A. purpurascens* Mett. ex Kuhn

8b. Pinnae entire to serrate, sometimes with a basal auricle on the acroscopic side and/or basiscopic side.

9a. Pinnae 7–11 × 1.2–2 cm, 6–9 pairs; petiole and rachis stramineous to greenish brown; southern Mexico to Venezuela and Peru, Cuba ..... 1. *A. delitescens* (Maxon) L. D. Gómez

9b. Pinnae 2–6 × 0.6–1.2 cm, 10–25 pairs; petiole and rachis atropurpureous; Mexico to southern Brazil ..... 3. *A. laetum* Sw.

leaf length, stramineous to green-brown, occasionally partly purplish, glabrous; lamina 20–30 cm long, green, 1-pinnate, deltate with an abruptly reduced, pinnatifid apex; rachis like the petiole, grooved and with herbaceous green wings; lateral pinnae 7–11 × 1.2–2 cm in the middle of the leaf, 6–9 pairs, lanceolate to linear-lanceolate, long-acuminate, the margin slightly toothed, the teeth 0.5–1 mm deep, excavate on the basal basiscopic side ⅙–¼ of the total length, acroscopic base truncate, auricle 1–4 mm long; veins 2-forked; sori 5–10 mm long, occasionally diplazioid in the abruptly reduced pinnae near the apex; spores 33–38 μm long, 64 per sporangium, perispore cristate.

*Additional specimens examined.* MEXICO. CHIAPAS: Mpio. de Ocosingo, ruins of Yaxchilán on the banks of the Río Usumacinta, 300 m, *Breedlove 29935* (F, MO, NY); Mpio. de Las Margaritas, W side of Laguna Miramar E of San Quintin, 350 m, *Breedlove 33123* (F, MICH, NY); Mpio. of Las Margaritas, low ridges at the confluence of the Río Ixcan with the Río Lacantum (Río Jatate) on the Guatemala border, 300 m, *Breedlove & McClintock 34140* (MO); Palenque, in rocky streamside forest by the ruins, 170 m, *Chater et al. 128* (BM, MO); Mpio. Ocosingo, 3 km S de Frontera Corozal, sobre la orilla del Río Usumacinta, 120 m, *Martínez S. 8008* (MO); Mpio. Ocosingo, en la zona Marquez de Comillas, a 6 km SE de Ejido Benemérito de las Americas, con rumbo a Flor de Cacao, 160 m, *Martínez S. 8136* (MO, NY); 24 km al SE de Crucero Corozal, camino Palenque–Boca Lacantum, 200 m, *Martínez S. 8402* (MO); Mpio. Ocosingo, 16 km NW de Boca Lacantum a Palenque, 220 m, *Martínez S. 16399* (MO); Cerro de Macuspana, *Rovirosa 1038* (GH), *3135* (MO); Ruina Palenque, 100 m, *Saiki M234* (F, Z). OAXACA: Mpio. Sta. María Chimalapa, a pie de la Piedra Siniguichi en la cabecera del arroyo Huahuagtza, cerca de Piedra Blanca, 7 km E de Sta. María, 270 m, 16°55′N, 94°37′W, *Hernández G. 734* (MO, NY); filo del cerro al E del Arroyo Monte Rico, ca. 20 km al E de Sta. María, 400–500 m, 16°55′N, 94°42′W, *Hernández G. 1574* (MO, NY); ca. 25 km al E de Sta. María, cerro al N de la unión del Río Blanco (del S.) con el Río del Corte, al N del Río del Corte, 400–500 m, 16°55′N, 94°42′W, *Hernández G. 1920* (NY); ca. de 18 km NE de Sta. María por la vereda al Río Pinal, Chimalapilla, 300 m, 16°57′N, 94°36′W, *Hernández G. & González L. 1787* (MO); Dtto. Tuxtepec, 9 km S of Tuxtepec and 4 km W of Rte. 175, behind Fabricas de Papel Tuxtepec, 100 m, *Mickel 5784* (NY, UC); between Tuxtepec and Playa Vicente, 28 km SE of Rte. 147, 100 m, *Mickel 7212* (NY, UC); Dtto. Juchitán, 1 km N of Palomares, 1 km E of highway on road to La Pedrera "Paso de Buques," 100 m, *Mickel & Pardue 6843* (NY, UC); 5 km S of Palomares, 150 m, *Mickel & Pardue 6866* (NY). TABASCO: Teapa, 4 km SE of Teapa on road to Tacotalpa, base of Cerro de Madrugal, 300 m, *Croat 47908* (CR, MO). VERACRUZ: Córdoba, *Finck 159* (UC); Mpio. Hidalgotitlán, near Campamento La Laguna, 100 m, 17°17′N, 94°30′W, *Nee 29974* (F); Mpio. Hidalgotitlán, entre Hermanos Cedillo y La Escuadra, Río Solosúchil, 150 m, *Vásquez 977* (NY); 2 km al N del Poblado no. 2, zona de Uxpanapa, Mpio. Jesús Carranza, 100 m, *Vásquez T. 2485* (NY). BELIZE. STANN CREEK: Stann Creek railway, 17 mi., *Gentle 2714* (F, GH, MICH, NY); caves and railway, 33 m, *Schipp 8-275* (B). TOLEDO: Columbia Forest Reserve, ca. 1–2 mi. N of entrance, *Croat 24173* (MO); Condemn Branch Hills, *Gentle 5139* (GH, MO, S); in cohune ridge, Chavarrias road, Resemederes, across Columbia River, *Gentle 6261* (F, G, NY, S, UC). GUATEMALA. PROV. UNKNOWN: Los Amates, 30 m, *Deam 470* (GH), *Smith 5675* (NY). PETEN: ca. 4 km S of Lacandón, *Contreras 3432* (MICH, S); Chinchilá, Sebol Road, *Contreras 10500* (F); along Río San Diego, between Finca Yalpemech and San Diego, 50–150 m, *Steyermark 45308* (F). HONDURAS. ATLANTIDA: Lancetilla Valley, near Tela, 20–600 m, *Standley 54153* (F). COPAN:

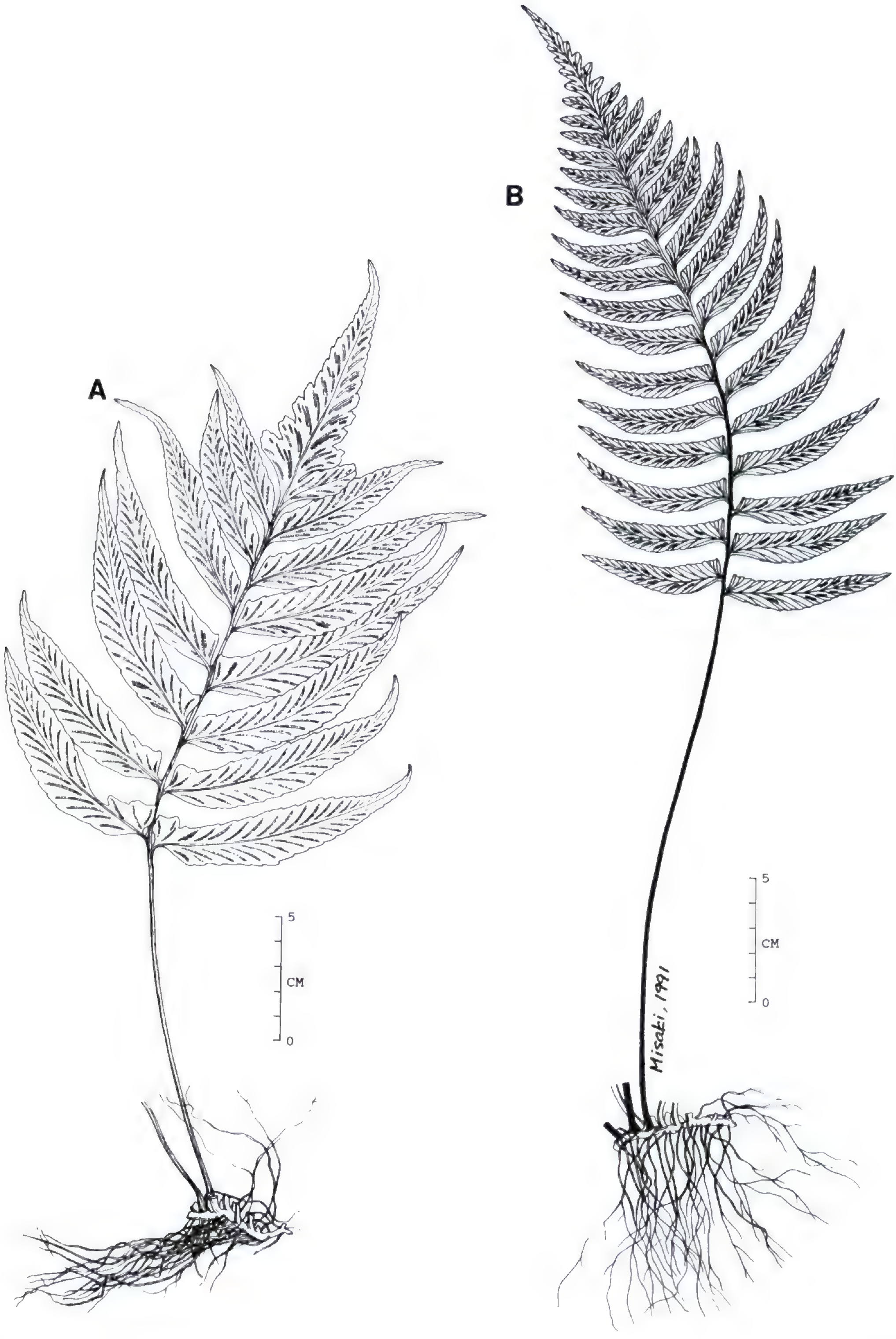
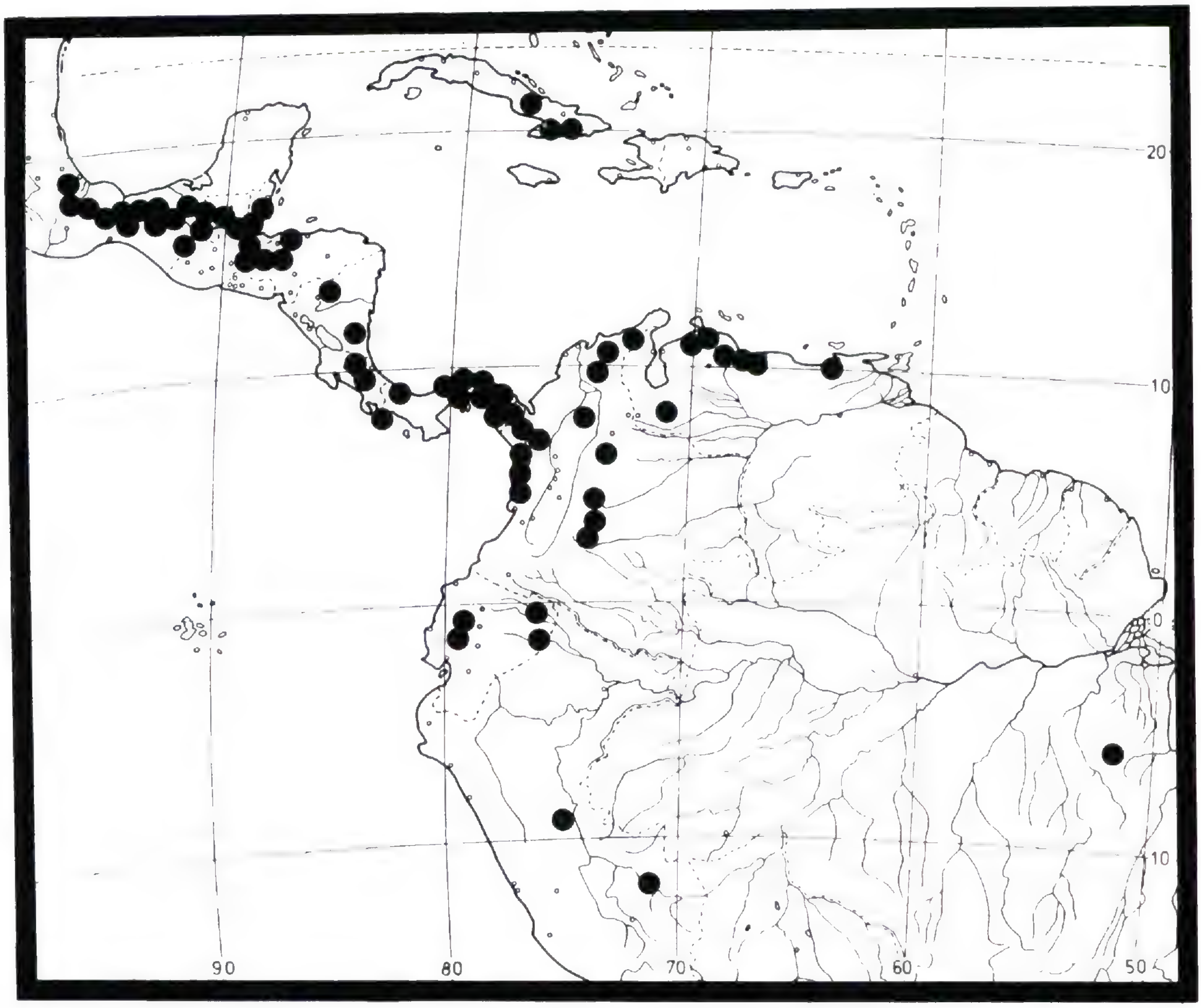



FIGURE 6.—A. *Asplenium delitescens*, Panama, *Seibert 583* (MO).—B. Possible hybrid between *A. delitescens* × *laetum*, Ecuador, *Luteyn et al. 8502* (NY).




MAP 2. The distribution of *Asplenium delitescens*.

20 km NW de Santa Rosa de Copán, hacienda Ocoteseco, 1,300 m, *Morales R. 65* (MO); Fort of La Cumbre, near creek, *Thieme 4* (UC); SANTA BARBARA: San Pedro Sula, 200 m, *Thieme 5675* (B, MO). NICARAGUA. MATAGALPA: El Carmen, carretera El Tuma a Waslala, 600–700 m, 13°13′N, 85°37′W, *Moreno 19063* (MO). ZELAYA: Dept. Bluefields, 3.6 km SE Cerro San Isidro, 65 m, 12°05′N, 83°45′W, *Proctor et al. 27114* (F). COSTA RICA. ALAJUELA: Aguacate, *Hoffmann 759* (B). SAN JOSE: Carrillo, 300 m, *Wercklé 17432* (B). PUNTARENAS: Palmar Norte, *Grayum et al. 9152* (MO, UC). PANAMA. BOCAS DEL TORO: vic. of Laguna de Chiriquí, *Hart 42* (UC). CANAL AREA: near Madden Dam, *Alston 8868* (BM); Barro Colorado Island, *Aviles 16* (F, MO); hill at Canal Zone boundary, vic. of Juan Mina, *Bartlett & Lasser 16580* (GH, MICH, MO); no locality, *Cornman 5121* (MICH); Colón to Empire, Panama Railroad, *Crawford 554* (BM, NY); Barro Colorado Island, Creek no. 8 S from Shannon Trail, growing in stream bed, *Croat 5192* (MO); Lutz Creek bank, *Croat 6516* (MO); Barro Colorado Island, Wheeler Trail 13, *Croat 8053* (MO); short cut to Lutz Trail behind animal house, *Croat 8515* (F, MO); Nemesia Trail 200, *Croat 8597* (MO); Armour Trail 2170, *Croat 8643* (F, MO); Barro Colorado Island, Armour Trail 850, *Croat 9425* (MO); Barro Colorado Island, Armour Trail 1040, *Croat 11639* (MO, NY); Barro Colorado Island, Drayton Trail 100, *Croat 12662* (MO); Barro Colorado Island, Armour Trail 500, *Croat 14056* (MO); vic. of Madden Lake along Boy Scout road, 100 m, *Croat 38327* (MO); Río Providencia 3 km SE of Achiote near W border of Canal Zone, 5–100 m, *Gentry 8679* (AAU, MO); *Hunnewell 16375* (MICH); Pipeline road, Limbo Hunt Club, *Kennedy & Andrews 1876* (MO); Barro Colorado Island, *Kenoyer 29* (GH); Valley of Masambí, on the road to Las Cascadas Plantation, 20–100 m, *Maxon 4677* (BM, GH, NY); Barro Colorado Island, Lake Gatún, *Maxon et al. 6807* (GH); trail along Río Petipie from road to Fort Sherman from Gatún Locks, *Mori & Kallunki 2672* (MO); 6 km E of Gamboa, headwaters of Río Casaya, *Nee 9026* (UC); Madden Dam, near Río Chagres, 50–75 m, *Seibert 583* (GH, MO); 4 mi. NE of Gamboa, vic. of Gold Creek, *Seibert 587* (F, MO); Barro Colorado Island, *Shattuck 189* (F, MO); Allison Armour trail, *Wetmore & Woodworth 105* (GH); Madden Lake, *Witherspoon & Witherspoon 8797* (MO). CHIRIQUI: Burica Peninsula, 8 mi. W of Puerto Armuelles, 200 m, *Croat 22493* (F, MO). COLON: ca. 6 km N of Chilibre, along shores of Madden Lake, 25–50 m, 9°12′N, 79°36′W, *Knapp 2716* (MO). DARIEN: near the mouth of Río Yape, 20 m, *Allen 347* (MO); Río Chico, from Yavisa at junction with Río

Chucunaque to ca. 1 hour by outboard from junction, *Burch et al. 1095* (MO); E slope of Cerro Sapo, 500 m, *Hammel 1266* (MO); Paya to Pucra, *Stern et al. 235* (F, GH, MO); vic. of Campamento Buena Vista, Río Chucunaque above confluence with Río Turquesa, *Stern et al. 824* (MO), *Tyson et al. 4835* (MO); 2 mi. E of Santa Fé, *Tyson et al. 4835* (UC); 2 km E of Juan Díaz, *Cornman 512* (MICH, MO, UC); Piriati, S of Pan American Hwy., 200–400 m, 9°00′N, 78°30′W, *Hamilton 529* (MO, UC); 1859–1861, *Hayes 57* (BM, F, GH); Bajia Sta., *Hayes 355* (BM, K); Juan Díaz, Topia River, 50 m, *Killip 2708* (B, MICH, S), 50 m, *Killip 2806* (MO); Gatuncillo River, *Rowlee & Rowlee 415* (NY); Panama Viejo?, *Seemann 66* (BM); Marraganti and vic., 0–60 m, *Williams 1026* (NY). PANAMA: Campana Hill, 800 m, *Alston 8925* (BM); Isla de Bayano, trocha D, *Correa A. et al. 2973* (F, MO); near Juan Díaz, 0–75 m, *Killip 2512* (S); Serranía de Majé, ridges S of Chocó village of Ipeti, Río Ipeti drainage system, 500–600 m, 8°47′N, 78°27′W, *Knapp & Sytsma 2334* (AAU, CR, MO); Chilibre, *Martínez 9* (MO); Río Bayano a 5 km del Camp. de Majé, *Rivera 23* (CR); Río Tapia, *Standley 26184* (MO). CUBA. ORIENTE: Sierra de Nipe, ad cañon fluminis Canapú, *Ekman 2533* (G, NY, S); near Bayate, Cayo del Rey, *Ekman 2760* (S).VENEZUELA. ARAGUA: Colonia Tovar, *Fendler 143* (G, NY). BARINAS: along Río Caparo, 2–4 km up river from dam site, 100–200 m, 7°41′N, 71°28′W, *Liesner & González 9473* (MO). FALCON: Parque Nacional Quebrada el Toro, 600 m, *van der Werff 402* (UC). LARA: border area between Edo. Lara/Yaracuy, Sierra de Aroa, 10–13 mi. NW of Urachiche along dirt road leading NW from Urachiche to Duaca, 1,400 m, 10°14′N, 69°04′W, *Smith et al. 1340* (MO). SUCRE: Dtto. Sucre, along Quebrada el Tigre, S of Fila La Baqueta (in the future basin of Represa Neveri), 350 m, 10°07′N, 64°19′W, *Davidse & González 19242* (MO, NY, UC). TERRITORIO FEDERAL AMAZONAS: upper Orinoco region, Ugueto, *Croziat 794* (BR). COLOMBIA. ANTIOQUIA: Guapá, 53 km S of Turbo, 60 m, *Haught 4628* (COL); 53 km S of Turbo, Guapá, 80 m, *Haught 4684* (NY, S). BOLIVAR: Boca Verde, on Río Sinu, 100–300 m, *Pennell 4213* (GH); 12 km S of Carraipia, Com. Guajira, 450 m, *Haught 4286* (COL, NY). CHOCO: near Caserío La Teresita, 0.5–2.5 km N of the INDERENA camp on the Río Truando, 50–100 m, *Lellinger & de la Sota 532* (COL); Nercua and Divide, *Schott 57* (F); Parque Nacional Natural Los Katíos, sector Cacarica, *Zuluaga R. 986* (COL). MAGDALENA: ca. 6 km E of La Jagua, Sororia Creek, 200 m, *Haught 3613* (COL); Santa Marta, *H. H. Smith 2693* (NY). SANTANDER: vic. of Puerto Berrio, between Carare and Magdalena rivers, 100–700 m, *Haught 1715* (COL, GH); SE of Puerto Berrio, 100 m, *Haught 2865* (COL, GH, UC). ECUADOR. LOS RIOS: Canton Vinces, Jauneche Forest, between Mocachi and Palenque, on Estero Peñafiel, 70 m, *Dodson et al. 7089* (AAU, MO, QCNE). MANABI: on road from Quevedo to Calceta, Hacienda Aurora, 400 m, *Haught 2976* (GH, S, UC). PERU. HUANUCO: Tingo María, on steep rocky slope above Río Huallaga, 650 m, *Croat 21075* (MO); along road from Tingo María to Monzón, vic. of Río Patay Rondos, Cuevas de Gucharo "Parque Nacional Tingo María," 650 m, *Croat 57945* (MO); hills above river on steep limestone forested slope, *Moran 3676* (MO); Pachitea, Dtto. Puerto Inca, Bosque Nacional de Iparía, 400–500 m, *Schunke V. 2967* (F). BRAZIL. PARA: Serra dos Carajás, ca. 6 km NW of AMZA camp 3-Alfa, on the road to camp 4-Alfa, 200–250 m, 5°47′S, 50°34′W, *Sperling et al. 6035* (GH, NY, UC); 12 km W of camp ECB on the ferrovia, ca. 57 km W of road BR 150, 150 m, 5°35′S, 49°15′W, *Sperling et al. 6381* (BM, F, GH, NY).

*Asplenium delitescens* occurs from Mexico to Peru and east-central Brazil, and Cuba (Map 2). It grows terrestrially in wet forests from 0 to 800(–1,400) m. Rarely, it grows on rocks.

The species is characterized by stramineous or greenish petioles, few (6–9) pinna pairs, and deltate laminae with abruptly reduced apices (Fig. 6A). Where the lamina abruptly contracts to the narrowed apical segment, the pinnae and lobes are often retuse. Occasional specimens are intermediate between *A. delitescens* and *A. laetum* (Fig. 6B). These are treated in the hybrid section of this monograph.

*Asplenium delitescens* closely resembles *A. abscissum* Willd. (which is not a member of section *Hymenasplenium*) in leaf cutting and outline. To the naked eye, *A. abscissum* differs from *A. delitescens* by its erect (rather than creeping) rhizome and the obovate, evenly serrate (rather than quadrangular-truncate, and irregularly serrate) pinnae that are immediately beneath the apical segment. Two microscopic characters also distinguish the species. Both species are sparsely scaly abaxially where the pinnae join the rachis. In *A. abscissum*, the scales are 0.2–0.6 mm long, reddish, and uniseriate. In *A. delitescens*, the scales are 0.5–1.5 mm long, blackish, and uni- to triseriate. The structure of the pinna and rachis is also diagnostic. *Asplenium abscissum* has a slightly raised costa and a thickened pinna margin decurrent on the side of the rachis (Fig. 16C). In contrast, *A. delitescens* has a slightly sunken costa bordered by a green flange of tissue that is decurrent on the adaxial surface of the rachis (Fig. 16D). The decurrent margin of the pinna is not thickened (this form of the rachis and costa juncture is constant throughout section *Hymenasplenium*).

Smith (1976) first pointed out that *A. delitescens* and several other neotropical *Asplenia* belonged to section *Hymenasplenium*. He also realized that this species belonged to *Asplenium*, rather than *Diplazium* where it was originally placed, and gave an excellent discussion on the characteristics that distinguish the two genera.

**2. Asplenium hoffmannii** Hieron., Hedwigia 60: 258. 1919. TYPE: Costa Rica. Alajuela: Aguacate, Aug. 1857, *Hoffmann 836* (holo-

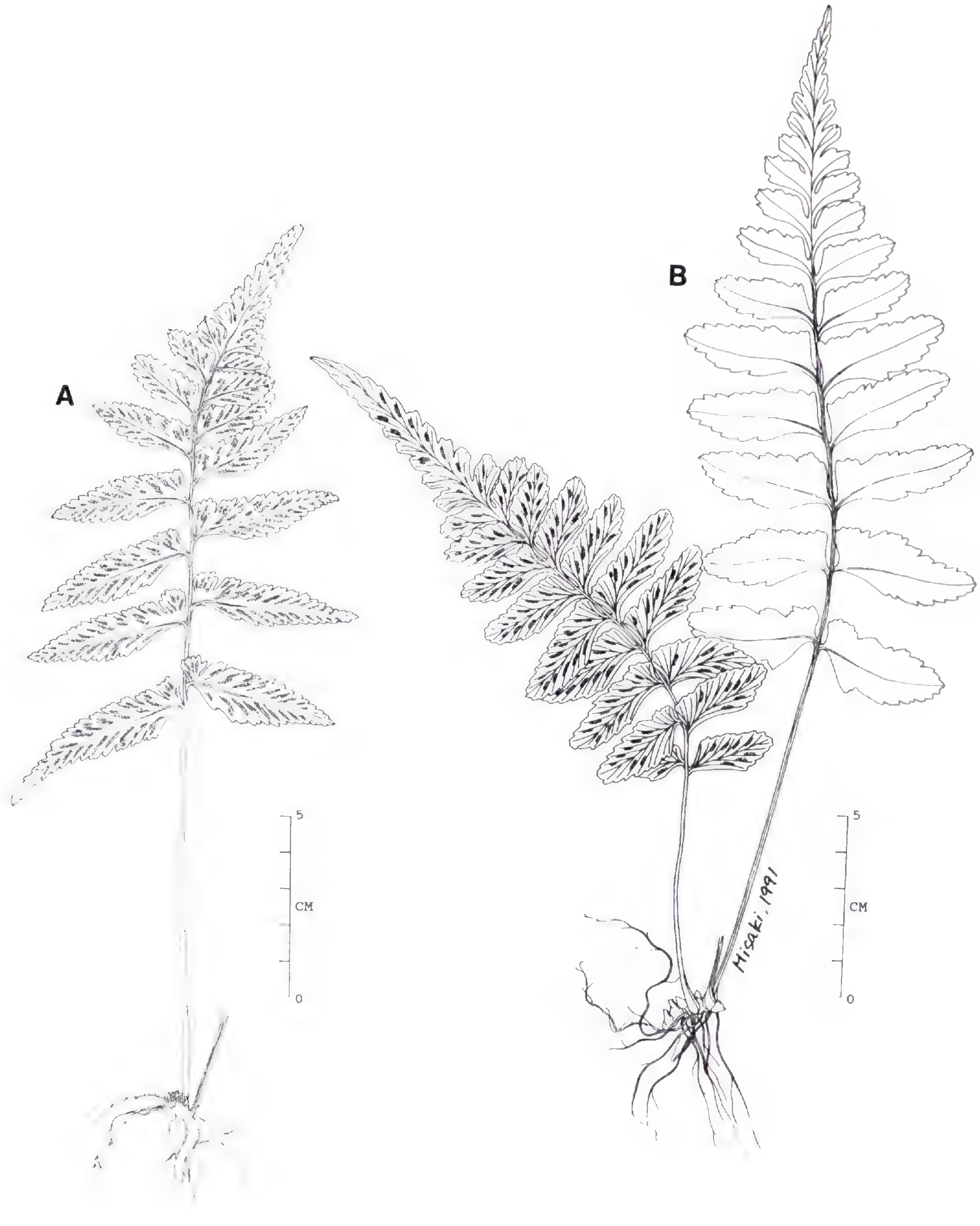
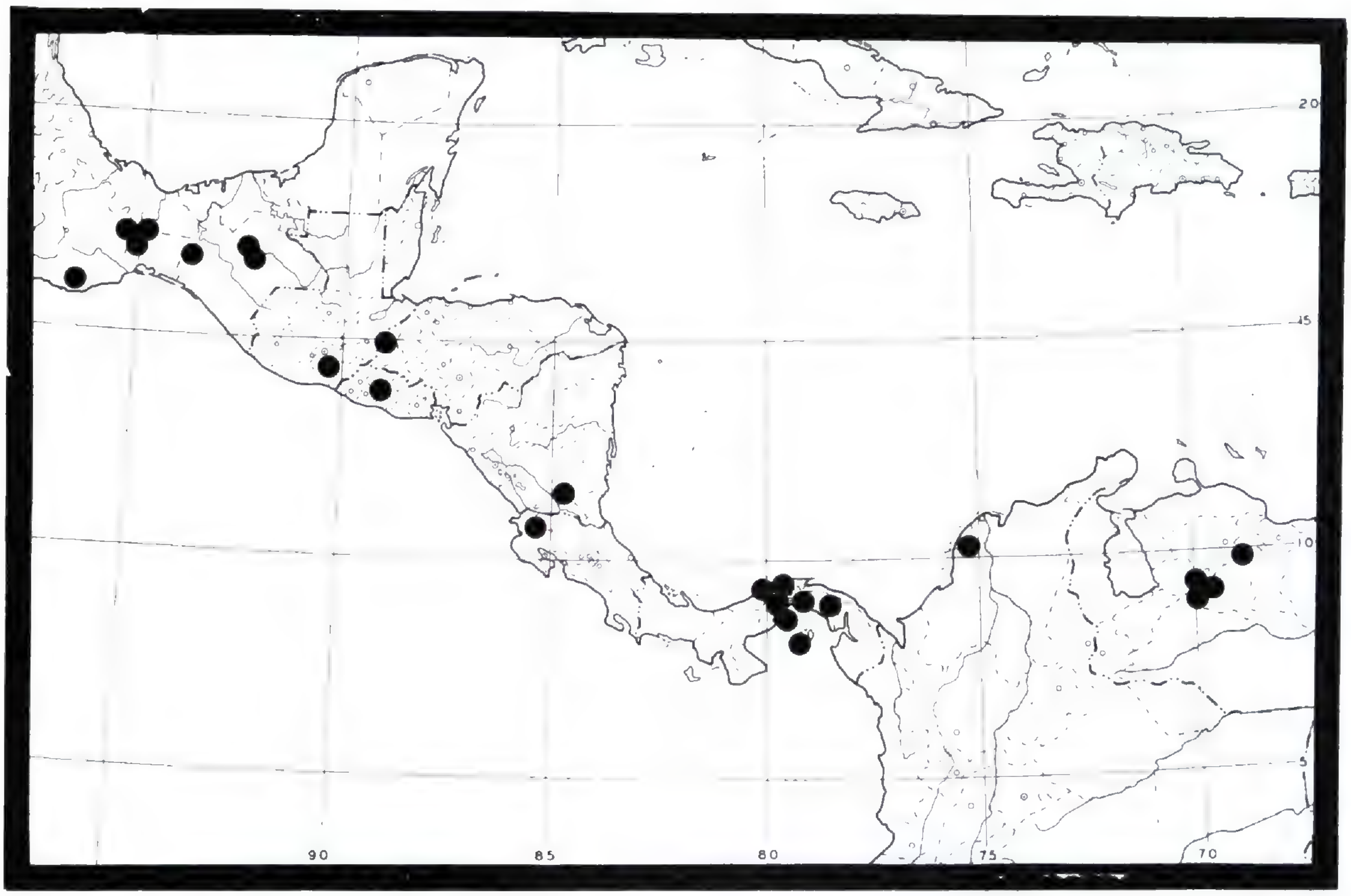



FIGURE 7. *Asplenium hoffmannii*.—A. Panama, *Johnston 131* (US).—B. Mexico, *Breedlove 33893* (MO).

type, B; isotype, NY fragment, photo BM ex B). Figure 7; Map 3.

*Asplenium membranifolium* Maxon, Amer. Fern J. 24: 72. 1934. TYPE: Panama. Panamá: ca. 10 mi. E of Panama City, *Killip 2567* (holotype, US; isotype, NY fragment).

Plants epilithic, rarely terrestrial; roots 0.4–0.6 mm wide; rhizome 1.8–3.5 mm wide, almost naked; scales 0.8–1.3 × 0.2–0.3 mm, black-brown, ovate-lanceolate; petiole base 1.4–2.4 mm wide, swollen, 0.3–2.7 mm distant from each other on the same row; petiole 4–9 × 0.05–0.1 cm, ¼–½ the leaf length, greenish, glabrous; lamina 15–40 cm long, light green, membranaceous, 1-pinnate,




MAP 3. The distribution of *Asplenium hoffmannii*.

lanceolate to oblong with attenuate apex; rachis green, grooved, with perpendicular wings; lateral pinnae 2–3.5 × 0.7–1.1 cm in the middle of the leaf, 2–6(–8) pairs, subquadrangular to lanceolate, the margin deeply toothed, 1–2 mm deep, excavate for ca. ½ the length of the basiscopic side, obtuse to acute at apex, shortly stalked at lower pinnae, auricle absent; veins 1–2-forked; sori 3–5 mm long; spores 33–38 μm, 64 per sporangium, perispore cristate.

*Additional specimens examined.* MEXICO. CHIAPAS: Mpio. of Ocosingo, ruins of Yaxchilán on the banks of the Río Usumacinta, 300 m, *Breedlove 33893* (MO); ruins of Yaxchilán on banks of the Río Usumacinta, 300 m, *Breedlove 42851* (MO); Tuxtla–San Andrés, *Schmid s.n.* (Z). OAXACA: Mpio. Sta. María Chimalapa, ca. 5 km N de Sta. María, Arroyo Mactaspac, cerca del Río del Corte, 200 m, 16°56′N, 94°41′W, *Hernández G. 2021* (NY); Dtto. Pochutla, 29.6 km NE of Pochutla, Oaxaca–Pochutla road, 300 m, *Mickel 1304* (NY); Dtto. Juchitán, 10–15 km W of Rte. 185, road from near Palomares toward Tuxtepec, 100 m, *Mickel 7411* (NY, UC); Dtto. Pochutla, 15 km N of Pochutla, 300 m, *Mickel & Leonard 5138* (NY); Juquila, 34 km N of Puerto Escondido, 500 m, *Mickel 6077* (NY). GUATEMALA. SANTA ROSA: near Oratorio, 1,200 m, *Standley 60656* (F). HONDURAS. COPAN: Ruinas de Copán, *Bernoulli 834* (B), *Bernoulli & Cario 290* (B, K). EL SALVADOR. PROV. UNKNOWN: El Salto near Huizuca, Río Las Lajas, 300 m, *Seiler 718* (NY). NICARAGUA. RIO SAN JUAN: San Bartolo, *Seymour 6200* (MO). COSTA RICA. GUANACASTE: 4 km W Bagaces, *Opler s.n.* (CR). GUANACASTE: Rincón de la Vieja National Park, slopes of Volcán Santa María, 700–900 m, 10°46′N, 85°18′W, *A. R. Smith et al. 1961* (CR, MO, UC). PUNTARENAS: Palmar Norte, *Grayum et al. 9159* (MO, UC). PANAMA. CANAL AREA: Juan Mina, Flat Rock, Chagres River, *Bartlett & Lasser 16843* (GH, MICH, MO); Alajuela, *Cornman 548* (MICH, UC); Fort Sherman, *Dwyer 6823* (MO); trail along Río Petitpie, from road to Fort Sherman from Gatun Locks, *Mori & Kallunki 2670* (MO); near Gatú, hills W of the Canal, *Standley 27218* (L, MICH, NY, UC); 1 mi. N of Summit Garden, on rock embankment of bridge just above small creek, *Sytsma 2314* (MO); Old Fort San Lorenzo, from rocks near fort in shade, 10 m, *Tyson 2237* (MO); Madden Forest Preserve, across from George W. Green Park, *Welch 19856* (MO); vic. of Salamanca Hydrographic Station, Río Pequení, 80 m, *Woodson et al. 1601* (GH, MO). COLON: ca. 6 km N of Chilibre, along shores of Madden Lake (Lago Alajuela), 25–50 m, 9°12′N, 79°36′W, *Knapp 2686* (MO); Panamá Viejo, *Seemann 72* (BM; photos GH, UC); Taboga Island, *Cornman 597* (MICH, UC); San José Island, Perlas archipelago, ca. 55 mi. SSE of Balboa, *Johnston 131* (BM, GH, U), *258* (BM, GH), *385* (BM, GH); ca. 55 mi. SSE of Balboa, *Johnston 444* (GH); Panamá Viejo, *Seemann 369* (BM). PANAMA: Madden Dam, forest near spillway, at bottom of dam, 50 m, 9°13′N, 79°37′W, *Churchill 3851* (MO, UC); 5 mi. W of bridge over Bayano Lake, 200 m, *Hammel & D'Arcy 5106* (MO); Río Tecumen, *Standley 29372* (GH). TRINIDAD: Blue Basin, *Hombersley 257* (BM). VENEZUELA. ARAGUA: prope coloniam Tovar, *Fendler 61, pro parte* (NY, mixed with *Asplenium* ×*incisoserratum*).

PORTUGUESA: Dtto. Araure, Los Hijitos, entre Agua Blanca y San Rafael, 160 m, *Ortega & Aymard 2089* (UC); Dtto. Guanare, near Desembocadero, 400 m, *A. R. Smith et al. 856* (MO, UC); Dtto. Guanare, along road to San José de La Montaña, 500 m, 9°20′N, 69°43′W, *A. R. Smith et al. 1095* (NY, UC); NE de Boca de Monte, 28–32 km NNE de Guanare, arriba del puente sobre el Río María, 400–500 m, 9°18–19′N, 69°42–43′W, *Steyermark et al. 127064* (MO, UC); 7 km NE de Boca de Monte, 22 km NE del vado del Río Suruguapo, 45 km NE por la autopista Guanare–Ospino, en el sitio Las Marías, E de Guanare, 400 m, 9°19′N, 69°41′30″W, *Steyermark et al. 127236* (MO, UC). COLOMBIA. BOLIVAR: Torrecilla, near Turbaco, 150–300 m, *Killip & Smith 14658* (K, NY).

*Asplenium hoffmannii* occurs from southern Mexico to Colombia, Venezuela, and Trinidad (Map 4). It grows on rocks along deeply shaded streams in wet forests. Rarely, it grows on old walls or terrestrially. The elevation ranges from 0 to 500(–900) m.

The species is characterized by membranaceous laminae, few (1–3) leaves per rhizome, deeply and evenly serrate pinnae, and few (usually 2–6) pinna pairs (Fig. 7). It hybridizes with *A. laetum* to produce *A.* ×*incisoserratum* (which see; Fig. 16). The hybrid differs from *A. hoffmannii* by having more pinna pairs (6–14), more than three leaves per rhizome, basally darkened petioles (especially in large leaves), and aborted spores.

**3. Asplenium laetum** Sw., Syn. Fil. 79, 271. 1806. NEOTYPE (designated by Proctor, 1985): Schkuhr, Krypt. Gew. 1: 65, t. 70. 1809. Figure 8A; Map 4.

*Asplenium virens* Desv., Mém. Soc. Linn. Paris 6: 273. 1827, not C. Presl, 1825. TYPE: "America," *collector unknown* (P-Herb. Desv.; photos GH, US ex P).

*Asplenium schkuhrianum* C. Presl, Tent. Pterid. 107. 1836, nom. superfl. for *A. laetum* Sw. LECTOTYPE (designated by Morton & Lellinger, 1966): Venezuela. Distrito Federal: Caracas, *Bredemeyer s.n.* (W-Herb. Jacquin). This is probably the specimen used by Schkuhr (1809) in drawing his t. 70, which has been designated as the neotype of *A. laetum* (see above).

*Asplenium lugubre* Liebm., Mexic. bregn. 243 (seors. 91). 1849. LECTOTYPE (designated by A. R. Smith, 1981): Mexico. Veracruz: Baranca de Mirador, *Liebmann* [Fl. Mex. 322] (lectotype, C not seen; isolectotypes, B, K).

Plants terrestrial or epilithic; roots 0.5–0.8 mm wide; rhizome 2.5–6.5 mm wide, sparsely scaly; scales 2–3.3 × 0.23–0.33 mm, black-brown, linear-attenuate; petiole base 1.5–3.5 mm wide, swollen, 0.4–2.5 mm distant from each other on the same row; petiole 4–20 × 0.09–0.15 cm, ⅛–½ the leaf length, blackish reddish purple, sometimes green, grooved, sparsely scaly at base; lamina 15–40 cm long, 1-pinnate, lanceolate to oblong with attenuate apex; rachis like petiole, grooved and with green, perpendicular, herbaceous wings; lateral pinnae 2–6 × 0.6–1.2 cm in the middle of the leaf, 10–25 pairs, subquadrangular, the margin slightly to strongly toothed, the teeth 0.5–2 mm deep, the basiscopic side excavate basally for ca. ½ the pinna length, the apex acute, the base broadly cuneate and almost sessile to stalked, auricle 0–3 mm long; veins 1-forked; sori 2.5–7.5 mm long; spores about 27–38 μm, 64 per sporangium, perispore cristate.

*Additional specimens examined.* MEXICO. CHIAPAS: on the Guatemala border, Mpio. of Las Margaritas, low ridges at the confluence of the Río Ixcan with the Río Lacantum (Río Jatate), 300 m, *Breedlove 34197* (MICH, MO); Mpio. of Frontera Comalapa, 6–8 km E of Frontera Comalapa along road to Ciudad Cuauhtémoc, 1,000 m, *Breedlove 39059* (NY); 13 km N of Berriozabal, Mpio. de Berriozabal, 1,000 m, *Breedlove & Smith 21683* (F, MICH, MO, NY); Mpio. of Cintalpa, SE of Cerro Baul on the border with Oaxaca, 16 km NW of Rizo de Oro along a logging road to Colonia Figaroa, 1,600 m, *Breedlove & A. R. Smith 31319* (NY); los alrededores de la zona Arquelógica de Palenque, *Cabrera et al. 1938* (BM, MO); Palenque, in forest by the ruins, 170 m, *Chater et al. 131* (BM, MO); 1864–1870, *Ghiesbreght 426* (K); Finca Mexiquito, *Purpus 6735* (F, MO, UC), *Purpus 6765* (UC); Finca Irlanda, *Purpus 7241* (UC); Ruina Palenque, 100 m, *Saiki M-230* (F, Z). OAXACA: Mpio. Sta. María Chimalapa, Arroyo Piedra de Tigre, ca. 8 km al O de Sta. María, 220 m, 16°53′N, 94°43′W, *Hernández G. 1008* (NY); Chimalapilla, ca. de 18 km al NE de Sta. María por la vereda al Río Pinal, 300 m, 16°57′N, 94°36′W, *Hernández G. & González 1787* (NY); Dtto. Tuxtepec, 4–9 km S of Valle Nacional on Rte. 175, 200 700 m, *Mickel 5881* (NY, UC); Dtto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, trail E of Rte. 175 at Campamento Vista Hermosa toward Ladu, 500–650 m, *Mickel 6461* (NY, UC); Dtto. Ixtlán, 76 km N of Ixtlán de Juárez on Rte. 175, 5 km S of Vista Hermosa, Campamento La Esperanza, *Mickel 7188* (NY, UC); vic. of Cafetal Concordia, 400–650 m, *Morton & Makrinius 238* (F); Tuxtepec, above Jalapa de Díaz, 330 m, *Hallberg 1468* (NY), 400 m, *Hallberg 1471* (NY). TABASCO: cerro arriba del Ejido Zunu, Mpio. Tacotalpa, Ejido Zunu en el camino de la Est. Tacotalpa hacia Tapijulapa, 180 m, *Cowan & Magana 3139* (MO, NY); Tacotalpa, 3 km al E del ejido Lázaro Cárdenas, 50 m, *Cowan 2072* (NY); Teapa, 3 km E of Teapa, slope of Cerro las Campanas, ca. 50 km S of Villahermosa, 50–100 m, *Conrad et al. 2889* (MO); Cerro de Cocorrá, near Teapa, *Rovirosa 828* (NY). VERACRUZ: près Córdova, Chiquihuite, *Bourgeau 2151* (K, L, MO, NY); Mpio. Hidalgotitlán, 6 km E de Cedillo camino a La Laguna, 110 m, *Dorantes et al. 2555* (F, UC); Orizaba, 1855 m, *Müller 1835* (NY); in Dec. 1921, *Purpus 174* (Z); Mirador, Barranca de San Francisco, 1,000 m, *Ross 688* (BM). BELIZE. STANN CREEK: caves and railway, 30 m, *Schipp*

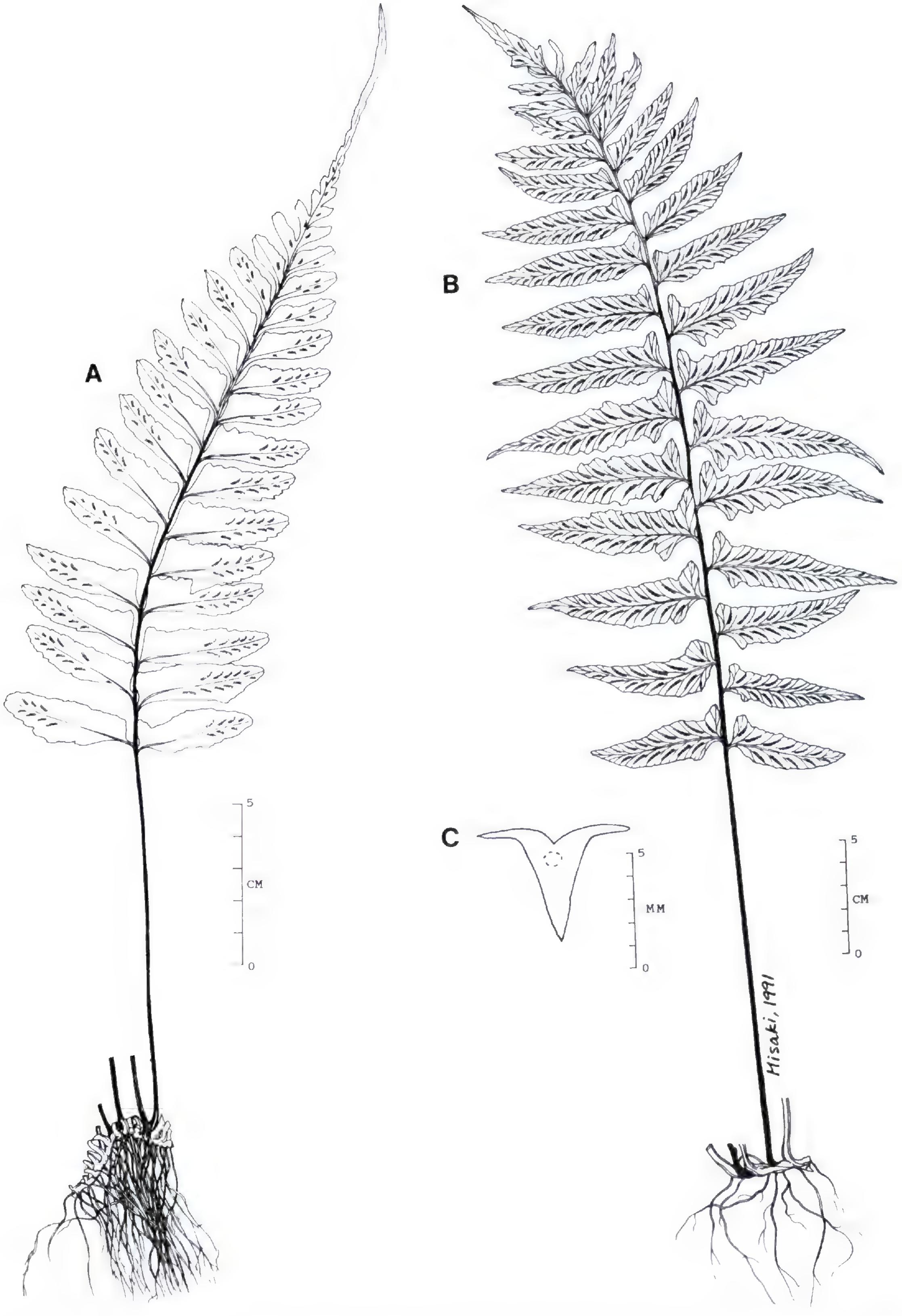
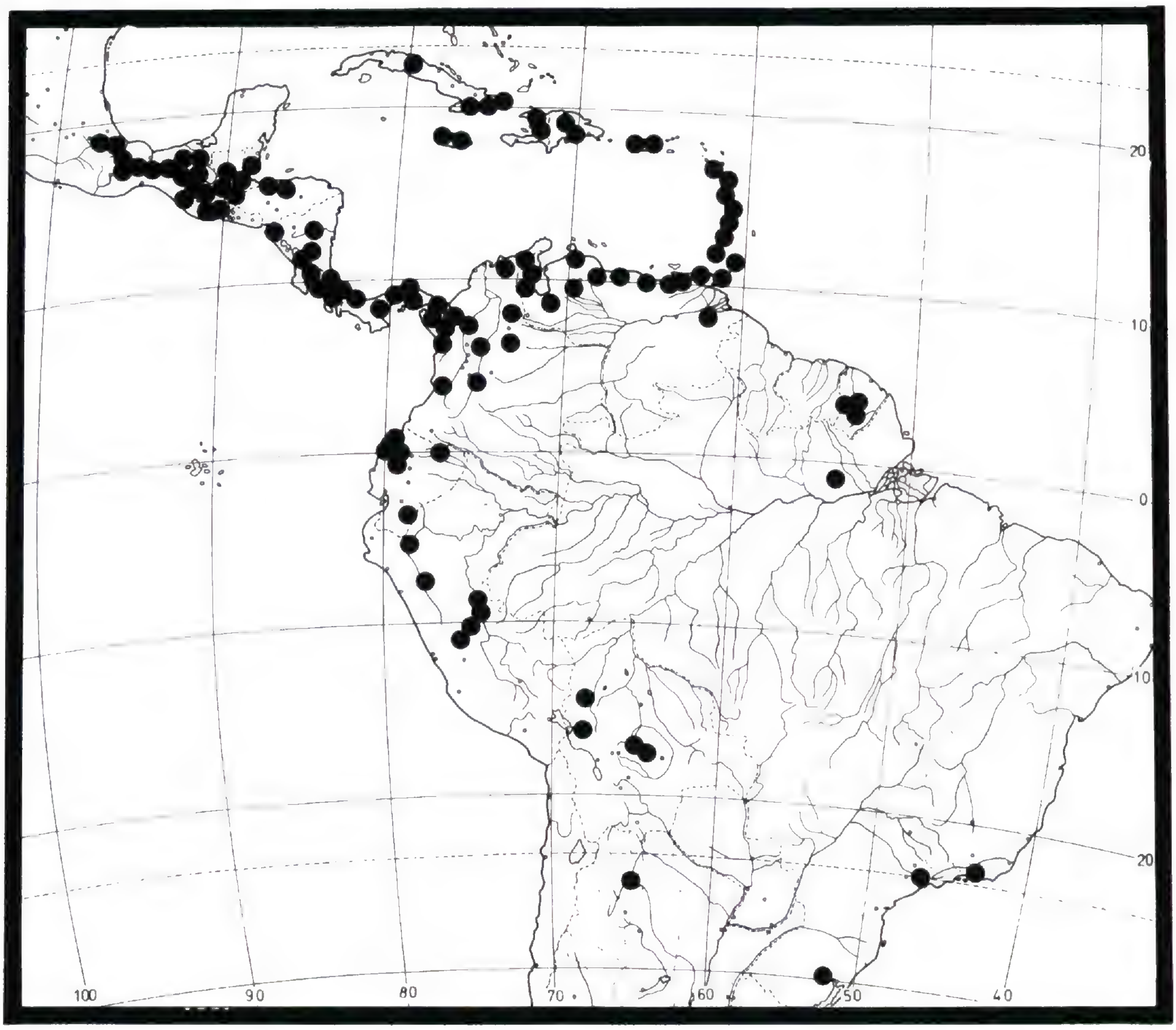



FIGURE 8.—A. *Asplenium laetum*, Panama, *Mori & Kallunki 2826* (MO).—B, C. *Asplenium triquetrum*, Brazil, *Dusén 6774* (MO). Cross section of rachis shown in C.




MAP 4. The distribution of *Asplenium laetum*.

*S-277* (B). TOLEDO: Edwards road beyond Colombia, on hilltop beyond Central camp, *Gentle 7378* (BM, F, G, MICH, NY, S, UC); Colombia Forest Reserve, vic. of forest camp ca. 6 mi. S of Cabro, in upper Río Grande drainage area, 300 m, *Proctor 36071* (BM, MO). GUATEMALA. ALTA VERAPAZ: Finca Mercedes, Teleman, Panzós, faldas da la Sierra de las Minas, quebrada Mercedes, 100 m, *Martínez S. et al. 22711* (MO); along Río Icvolaty, N and NW of Finca Cubilquitz to Quebrada Diablo, 300–350 m, *Steyermark 44752* (F); 1 mi. SW of Sibicte, vic. of Iaguana Sapala (Chajvovuch), 280 m, *Steyermark 44894* (F, UC). ESCUINTLA: SE of Escuintla, along or near Río Michatoya, 250–300 m, *Standley 89091* (F); between Panzós and Senahú, vic. of Cacão, 275 m, *Barber 6* (NY); Nazatenango, orillas del Río Grande, *Bernoulli 347* (B); Cubilquitz, *von Türckheim 8048* (B, NY, S). HUEHUETENANGO: Sierra de los Cuchumatanes, between Ixcan and Finca San Rafael, 200–800 m, *Steyermark 49389* (F). PETEN: W of Chinajá, along Río San Román, 50 m, *Steyermark 45507* (NY); along Río San Román, 50 m, *Steyermark 54407* (F); Sacatepequez, below Barranco Hondo, 1,100 m, *Standley 88974* (F). HONDURAS. ATLANTIDA: near Tela, Lancetilla Valley, 20–600 m, *Standley 52815* (F), *53554* (F); Mts. back of Puerto Sierra, *Wilson 161* (NY), *Wilson 577* (NY). NICARAGUA. CHINANDEGA: vic. of Chichigalpa, 90 m, *Standley 11234* (UC). CHONTALES: Castillo, Mar. 1893, *Shimek s.n.* (F, MO). MASAYA: Sierra de Managua, región de Las Nubes, *Standley 8744* (F). RIVAS: Isla de Ometepe, NW slope of Volcán Maderas, 800–1,000 m, 11°27′N, 85°31′W, *Stevens et al. 6582* (MO). ZELAYA: Cerro Baká, 6.5 km E of Río Coperna, 200–320 m, 13°40′N, 84°30′W, *Pipoly 4861* (MO). COSTA RICA. ALAJUELA: San Pedro de San Ramón, cerca del Río Barranca, *Brenes 21520* (CR). CARTAGO: Orosi, *Losch 770* (M); Finca Navarro, 1,350 m, *Maxon 623* (NY), *Maxon 641* (NY); 4 mi. SE of Turrialba, Las Animas RR station, 500 m, *Chrysler 5134* (MO, UC); near Río Naranjo, 2 km W of Orosi, 1,400 m, 9°48′N, 83°52′W, *Lent 4061* (AAU, CR, F, MO); Tapantí, ca. 15 km S of Paraíso, 1,150 m, *Mickel 1862* (NY), *2317* (NY); Carpintera, *Polakowsky 151* (B); Turrialba, slope of the Río Reventazón, behind the Instituto Interamericano de Ciencias Agrícolas, 600 m, *Mickel 2061* (NY), *3359* (NY). GUANACASTE: along Río Las Flores, between Quebrada Desprendimiento and Q. Sanguijuela, Hacienda Montezuma, 450 m, 10°40′N, 85°04′5″W, *Grayum et al. 4906* (MO). LIMON: near Río Sixaola ½ mi. SW of Bambú, ca. 3 mi. NE of Bratsi, 15 m, *Croat 43251* (MO, UC); lago sin nombre al pie de Fila Lleskila–Talamanca, 1,160 m, *Gómez et al. 23094* (AAU, BM,

MO, UC); base of hills on coastal side, between Punta Cocles and Punta Uva (E of Puerto Viejo de Talamanca), 20–60 m, 9°38′N, 82°43′W, *Grayum et al. 4419* (BM, MO, UC); Cordillera de Talamanca, ridge between Río Dantas (opposite mouth of Caño Seco) and Río Barbilla, 250–419 m, 10°00′5″N, 83°26′W, *Grayum et al. 8943* (MO); ca. 400 m upstream from where Bri Bri-Hone Ck. road crosses Río Sandbox, 70 m, *Moran 3092* (CR, F, MO); ca. 3 km SW of Suretka, RECOPE test drill site, 70 m, *Moran 3121* (MO); Chase, Talamanca, 300 m, *Ocampo S. 1637* (CR). SAN JOSE: ca. 7.5–8.5 km by road W of Ciudad Colón, ridge between Río Virilla and Quebrada Micos, along road between Finca Micos and Llano Limón, 550–650 m, 9°56′N, 84°18′W, *A. R. Smith et al. 1620* (MO, UC); 5 mi. S of Sta. María, 2,000 m, *Stork 1764* (MICH). PANAMA. CANAL AREA: near Frijoles, *Cornman 698* (UC); Barro Colorado Island, Shannon Trail, in creek no. 3, *Croat 8475* (F, NY); Frijoles, 30 m, *Killip 2810* (B, S), *2829* (S); along Río Indio de Gatún, 0–10 m, *Maxon 4868* (BM, S); Pipeline road, 8 km from main gate, *Mori & Kallunki 2826* (AAU, NY); 8 km NW of Gamboa, along Río Mendoza and small tributary, 0.5–1 km upstream from Pipeline Road bridge, 100 m, *Nee 7722* (U); 2–3.5 km N of Gamboa, along Quebrada San Antonio, 30–200 m, *Nee 9456* (AAU, U); Pearson Trail, *Shattuck 283* (F). CHIRIQUI: vic. of El Boquete, 1,000–1,300 m, *Maxon 5055* (BM, NY, S). COCLE: El Valle de Antón, 1,000 m, *Alston 8707* (BM). COLON: N of Diamante, ridge NW of abandoned mine on Quebrada de la Mina, 600–700 m, 9°24′N, 79°35′W, *Churchill & de Nevers 4242* (MO); near Porto Bello, 5–200 m, *Maxon 5733* (NY). DARIEN: Parque Nacional del Darién, ridge between Río Topalisa y Río Pucuro, ca. 17 km E of Pucuro, La Laguna area, 750–850 m, 8°3′5″N, 77°17′W, *Cuadros V. et al. 3895* (UC); near Cerro Pirre base camp, on Río Parasenico, 200–500 m, *Gentry & Clewell 7064* (MO); on Río Parasenico, 200–500 m, *Gentry & Clewell 7069* (MO); RENARE hut in Darién Natl. Park, 20 m, *McDonagh et al. 446* (BM); bank above Río Paca, *Stern et al. 705* (BM, NY, UC). PANAMA: at Río Tito, Península de Panamá, 275 m, *Ekman 15271* (BM, NY, S); Cordillera Central, Los Haitises, La Llanada, *Ekman 15485* (F, G, NY, S); Sta. Bárbara de Panamá, Península de Panamá, *Ekman 15836* (K, S); Tapia River, vic. of Juan Díaz, *Killip 2710* (S). CUBA. LAS VILLAS: Trinidad Mts., Santa Clara, El Porvenir, 650–750 m, *Britton & Wilson 5300* (NY); San Blas, La Sierra, Prov. Sta. Clara, 200–300 m, *Jack 7093* (MO, NY). ORIENTE: Loma del Gato, *Clement 757* (K, MICH, S, U, UC); Prov. directly S of Jaguey, Yateras, 420–510 m, *Maxon 4158* (NY, S), *Otto 176* (K); El Yunque, Mt. Baracoa, *Underwood & Earle 615* (NY); Baracoa, El Yunque Mt., *Underwood & Earle 989* (NY); prope villam Monte Verde, *Wright 1026* (G, K, L, MO, NY, S, UC), *Wright 1027* (G, K, L, UC); in 1859, 1860, *Wright 1086* (BM, G, K). JAMAICA. PROV. UNKNOWN: Wingfield ravine, 100–300 m, *Proctor 19252* (BM, MICH, U); in 1895, *Gilbert 54* (NY); Dollwood, *Harris 7374* (K); 1,200 m, *Harris 7374* (BM, NY), *Jenman 24* (K); Hartford and adjoining properties, near Priestman's River, near Cudjoe's Hole, *Maxon 2545* (NY). ST. THOMAS: 500–700 m, *Maxon 9057* (NY); John Crow Mts., E of Seamen's Valley, Portland Parish, 200–425 m, *Maxon & Killip 244* (BM, F, NY). PORTLAND PARISH: valley of Trafalgar River, near Jumbe Spring, 800 m, *Maxon & Killip 772* (BM, F, NY); Chepston Ridge, above Mt. Hermon, 6 mi. inland from Hoper Bay, *Moore 7* (NY); Chepstow Ridge, St. Georges, *Moore s.n.* (NY); Moy Hall, *Orcutt 6835* (UC). TRELAWNY PARISH: 5 mi. N of Quick Step, above Aberdeen P.O., Cockpit country, *Proctor 4069* (MO); 1.5–2 mi. SW of Ecclesdown, E slope of the John Crow Mts., 500–600 m, *Proctor 22690* (BM, MICH, U); Doll Wood, near Silver Hill Gap, 1,000 m, *Underwood 2304* (NY); Mansfield, near Bath, *Underwood 2802* (NY). DOMINICAN REPUBLIC. Liali, 100–500 m, *Abbott 2627* (GH); ravine 0.2 mi. SE of S Chiltern Estate, 300 m, *Lellinger 517* (MICH, MO, UC); Santo Domingo, prope Barahona, 350 m, *von Türckheim 2824* (BM, G, K, L, M, NY); Cordillera Central, La Cumbre, 300 m, *Ekman 14338* (S). HAITI. Massíf du Nord, Morne Cheneau, near Poitean, 400 m, *Ekman 4430* (S); Massíf des Cahos, Hinche, Morne Vaillecite, 600 m, *Ekman 6106* (S); Massíf de la Tloffe, eastern group, Mt. Calumelle, 1,200 m, *Ekman 7332* (S); vic. of St. Louis du Nord, *Leonard & Leonard 14363* (NY); Port Margot to Correil, 400–500 m, *Nash 199* (NY). PUERTO RICO. Luquillo Mts., *Wilson 280* (F, NY). MONTSERRAT. In Oct. 1879, *Holme s.n.* (K). ST. KITTS. 1889, *Berkeley s.n.* (NY). GUADELOUPE. In 1868, *Husnot 338* (K), *L'Herminier 18* (K); bois du Maine Gommer, bod du Galion, 400–600 m, *Duss 4199* (NY). DOMINICA. *Imray 120* (K); Rosalie, *Lloyd 699* (NY); Trafalgar Falls, *Whitefoord 6164* (BM). MARTINIQUE. Hautenis boisies de la Riviere, 400–500 m, *Duss 1635* (NY). ST. LUCIA. Upper Roseau River, 300 m, 18 Feb. 1936, *Box 464* (BM); Nov. 1883, *Murray 26* (K). GRENADA. ST. MARK PARISH: NW slope of Mt. St. Catherine, 500–600 m, *Proctor 17250* (U); near trail to Concord Falls, 360 m, *Seifert 42* (Z); no locality, *Sherring 87* (K, NY). ST. VINCENT. ST. ANDREW PARISH: Lowrt, 400 m, *Cooley 8393* (S). PROV. UNKNOWN. *Jenman s.n.* (NY); *H. H. Smith 1362* (BM); in 1890, *Smith 358* (G); 1890, *H. H. Smith & G. W. Smith 1121* (K, NY); forest above S end of the island, 300 m, *H. H. Smith & G. W. Smith 961* (K). TOBAGO. Campbelton woods, Charlotteville, *Broadway 3026* (B, BM, F, G, MO, NY, S, Z); Castara woods, *Broadway 4212* (BM, G, K), *7180* (BM, F, K, MO, S, Z); in 1889, *Hart 4166* (K); near Parrot Hall, ca. 2 mi. SW of Parlatuvier, 50 m, *Jermy 11370* (BM); Blue Basin, *Johnston 161* (BM); forest reserve of Main Ridge, 300 m, *Sandwith 1833* (BM, NY). TRINIDAD. North Post to Maqueripe, *Britton et al. 909* (F); Maracas, in the ground near waterfall, *Broadway s.n.* (K); Camaron Waterfall, *Cruger 44* (B); Leotode Est. Oropouche, Cave Forest, on limestone hill, *Fay 665* (BM); no locality, *Hart 205* (S); Maracas Falls, *Johnston 74* (BM); Simla Research Station, ca. 4 mi. N of Arima, 250 m, *Mickel 9516* (NY); without locality, *Prestoe 714* (BM, MO). FRENCH GUIANA. ININI: Inini River, en aval de degrad Fourmi Camp de base vers les Monts de l'Inini, *Cremers et al. 8780* (B, BR, F, Z); Montagne de l'Inini, extremité NW, 550 m, 3°30′40″N, 53°36′W, *Cremers et al. 8900* (F, U, Z); Montagne de l'Inini, zone central, extremité NW, 350–400 m, 3°31′N, 53°35′W, *Cremers et al. 9314* (B, F, Z); Mont Galbao, Cirque central, Haute Crique Makouali, 350 m, 3°35′N, 53°18′W, *de Granville et al. 8947* (BM, F, NY, Z). VENEZUELA. ANZOATEGUI: NE of Bergantin, Quebrada Negra, tributary of Río Zumbador, 500 m, *Steyermark 61143* (F, MO). ARAGUA: prope Coloniam Tovar, *Fendler 136* (B, G, GH, MO, NY). BOLIVAR: limites con el Territorio Federal Delta Amacuro, 36 km al NW de El Palmar, 350 m, 8°25′N, 62°00′W, *Aymard C. 5274* (UC), *5297* (MO). DISTRITO FEDERAL: Caracas, Chacao, *Otto 609* (B, G, K). FALCON: Dtto. Silva, Hacienda Montesco-Silencio, ca. 10 km NW de Tucacas, Cerro

Sanare, 100 m, *Burandt 715* (UC); Dtto. Federación, Parque Nacional "Cuevas de la Quebrada El Toro," 500–600 m, *Quijada 103* (NY); Sierra de San Luis, arriba de la Chapa, 900 m, 24 Mar. 1979, *van der Werff 3403* (UC). MERIDA: Mérida, *Moritz 365* (B, BM). MIRANDA: Cerros del Bachiller, near E end, Quebrada Corozal, S of Santa Cruz, 20–65 m, 10°9′N, 65°48′W, *Steyermark & Davidse 116306* (MO, UC). PORTUGUESA: Dtto. Apure, en los rios Bocoy y Riecito, limite entre estados Lara y Portuguesa, 800–1,200 m, 9°37′N, 69°25′W, *Ortega & Aymard 1818* (UC); Dtto. Guanare, entre Chabasquen y Córdoba, 1,250 m, *Ortega & Stergios 1467* (UC); Dtto. Sucre, Los Paramitos, a 20 km por aire al SO de Biscucuy, 1,000–1,500 m, 9°20′N, 69°05′W, *Ortega et al. 1886* (MO, NY, UC). SUCRE: *Ortega et al. 1845* (MO); Dtto. Cagigal, near border with Dtto. Arismendi, 850 m, 10°39–40′N, 62°43′W, *Steyermark et al. 121514* (MO, NY, UC); in 1846, *Moritz 23* (G). ZULIA: Dtto. Mara, cuenca del Río Guasare, alrededores del Destacamento Guasare no. 1 (La Yolanda), 200–250 m, 10°52′N, 72°29′W, *Bunting et al. 12036* (UC); SW de Machiques, a lo largo de la Quebrada Perayra, afluente del Río Tokuku, SE de la Misión de Los Angeles de Tokuku, 450–475 m, *Steyermark 99872* (MO). COLOMBIA. ANTIOQUIA: near Guapá, 53 km S of Turbo, 60 m, *Haught 4627* (NY, S); Boquerón, *Kalbreyer 1916* (B); Titiribí, *Kalbreyer 1499* (B); Urrao, Vereda Calles, Parque Nacional de Las Orquídeas, cabana del INDERENA en Río Calles, quebrada La Agudelo, 1,450 m, *Callejas et al. 2841* (NY); Tocarema, 2,200 m, *Lindig 236* (BM). CHOCO: carretera San José del Palmar-Novita, entre La Italia (pueblo nuevo) y Curundo, 430–450 m, *Forero & Jaramillo 2134* (MO); near Caserío La Teresita, 0.5–2.5 km N of the INDERENA Camp on the Río Truando, 50–100 m, *Lellinger & de la Sota 550* (COL); Atrato, *Schott 51* (F, MO), *755* (MO); Parque Nacional Natural Los Katíos, sector Tilupo camino del Salto, *Zuluaga R. 332* (COL). MAGDALENA: Santa Marta, Finca El Recuerdo, Boca Toma Forest, 800 m, *Bennett 20* (F); Finca Los Arroyitos in quebrada N of house, 1,800–1,900 m, 10°56′N, 73°58′W, *Kirkbride 2368* (COL); 1,000 m, *H. H. Smith 2450* (BM, F, MICH), *958* (BM, MICH, S). CUNDINAMARCA: Pueblo Nuevo, quebrada "La Guayacana," 900–950 m, *Murillo 363* (COL). NORTE DE SANTANDER: Ocaña, 2,000 m, *Kalbreyer 317* (B, K); 1846–1852, *Schlim 397* (B, BM, G). SANTANDER: Espíritu Santo, 1,800 m, *Kalbreyer 317* (B). TOLIMA: Cajamarca, between Ibague and Cajamarca, 2,000 m, *Alston 7716* (MO). VALLE: La Margarita, Río Digua Valley, 760 m, *Killip 34888* (COL). ECUADOR. ESMERALDAS: near San Mateo, road to Esmeraldas airport, gravel road 8.6 km beyond bridge, over Río Esmeraldas, 80 m, 0°52′N, 79°33′W, *Croat 55623* (F, MO). LOS RIOS: Río Palenque Biological Station, km 56 Quevedo–Sto. Domingo, 150–220 m, *Evoy 61* (NY), *Lojtnant 15757* (AAU). MANABI: El Recreo, *Eggers 15118* (BM, F, L, M), *15175* (F). MORONA-SANTIAGO: cerca la Parroquia de Bomboiza, en la carretera Gualaquiza–Zamora, alrededores del puente sobre el Río Bombioza, 800 m, *Baker & Zaruma 6476* (MO, NY). NAPO: Parque Nacional Yasuní, Anangu, 260–350 m, 76°23′W, 0°31–32′S, *Øllgaard et al. 39205* (AAU, NY). PICHINCHA: Loc. 170–175, Sto. Domingo–Quinindé, 300 m, *Acosta S. 13783* (F). PERU. AMAZONAS: Bagua, 12 km E of La Peca, 1,700 m, *Barbour 2500* (F). HUANUCO: Leoncio Prado. La Cueva de las Pavas, 5 km S de Tingo María, Dtto. Rupa Rupa, 672 m, *Schunke V. 3261* (F); Tingo María, on steep rocky slope above Río Huallaga, *Croat 21082* (MO); hills above river on steep limestone forested slope, 650 m, *Moran 3683* (MO), 700 m, *Tryon & Tryon 5228* (BM, F). JUNIN: Cochero, 1,780 m, *Pavón 186* (G); Chanchamayo, 1,500 m, *Schunke 20* (S), *4909* (BM); area of Pichita Caluga, *Walden 84* (BM). PASCO: Oxapampa, 50 km from Oxapampa, Río El Tunqui, 1,620 m, 75°30′W, 10°15′S, *Smith et al. 1710* (MO). SAN MARTIN: Juan Jui, Alto Río Huallaga, 400–800 m, *Klug 4253* (BM, F, MO, NY, S). BOLIVIA. LA PAZ: Prov. Iturralde, Tumupasa, 500 m, *Williams 1076* (NY, UC); 600 m, *Williams 1076a* (NY). COCHABAMBA: Prov. Chapare, vic. of Villa Tunari, along Río Espírito Santo, on trail to Baja Copacabana, 16°57′S, 65°25′W, *Croat 51271* (MO). LA PAZ: Prov. Nor Yungas, Polo-Polo bei Coroico, 1,100 m, *Buchtien 3334* (S). BRAZIL. STATE UNKNOWN: no locality given, *Mendonca 1208* (B). PARA: Macau airstrip, 1.5 hours upstream from Lageira airstrip, on Rio Maicuru, 0°55′S, 54°26′W, *Strudwick et al. 3574* (NY). RIO GRANDE DO SUL: Sta. Cruz, *Jürgens 27* (MICH). RIO DE JANEIRO: Rio de Janeiro, *Glaziou 5318* (B). SÃO PAULO: São Paulo, *Mosen 3736* (S). ARGENTINA. SALTA: Parque Nacional El Rey, *Brown 1338* (MO).

*Asplenium laetum* grows terrestrially in deeply shaded forests or on boulders along streams. It is the most common and widely distributed species of section *Hymenasplenium* in the New World (Map 4), ranging from Mexico to northern Argentina, but absent from most of Amazonia. The species has sometimes been reported from Africa and Madagascar, but these reports are based on specimens of *A. inaequilaterale* Willd., a species that does not belong to section *Hymenasplenium*.

The species is characterized by dark petioles and rachises, short-creeping rhizomes, and attenuate lamina apices (Fig. 8A). In other characters it is extremely variable. Some single-character variation is correlated with geography. For example, plants from the Canal Area in Panama usually have obtuse or retuse pinnae with nearly entire or shallowly serrate margins (e.g., *Croat 7008*, *Kennedy 2673*, *Béliz 150*). Plants from Bolivia and Peru have attenuate pinna apices with sharply and obliquely serrate margins (e.g., *Croat 51271*, *Klug 4253*, *Schunke V. 3261*). We have not, however, subdivided the species because no other characteristics correlate with this variation, nor are there any suites of quantitative characteristics that correlate with geography (Fig. 9). Future studies, especially of isozymes and chromosomes, may show that *A. laetum* as circumscribed here actually consists of several species.

Occasional specimens will key to *A. laetum* that are actually intermediate between *A. delitescens* and *A. laetum* (Fig. 6B). Such intermediate specimens are treated in the hybrid section of this monograph.

Several species of *Asplenium* that do not belong

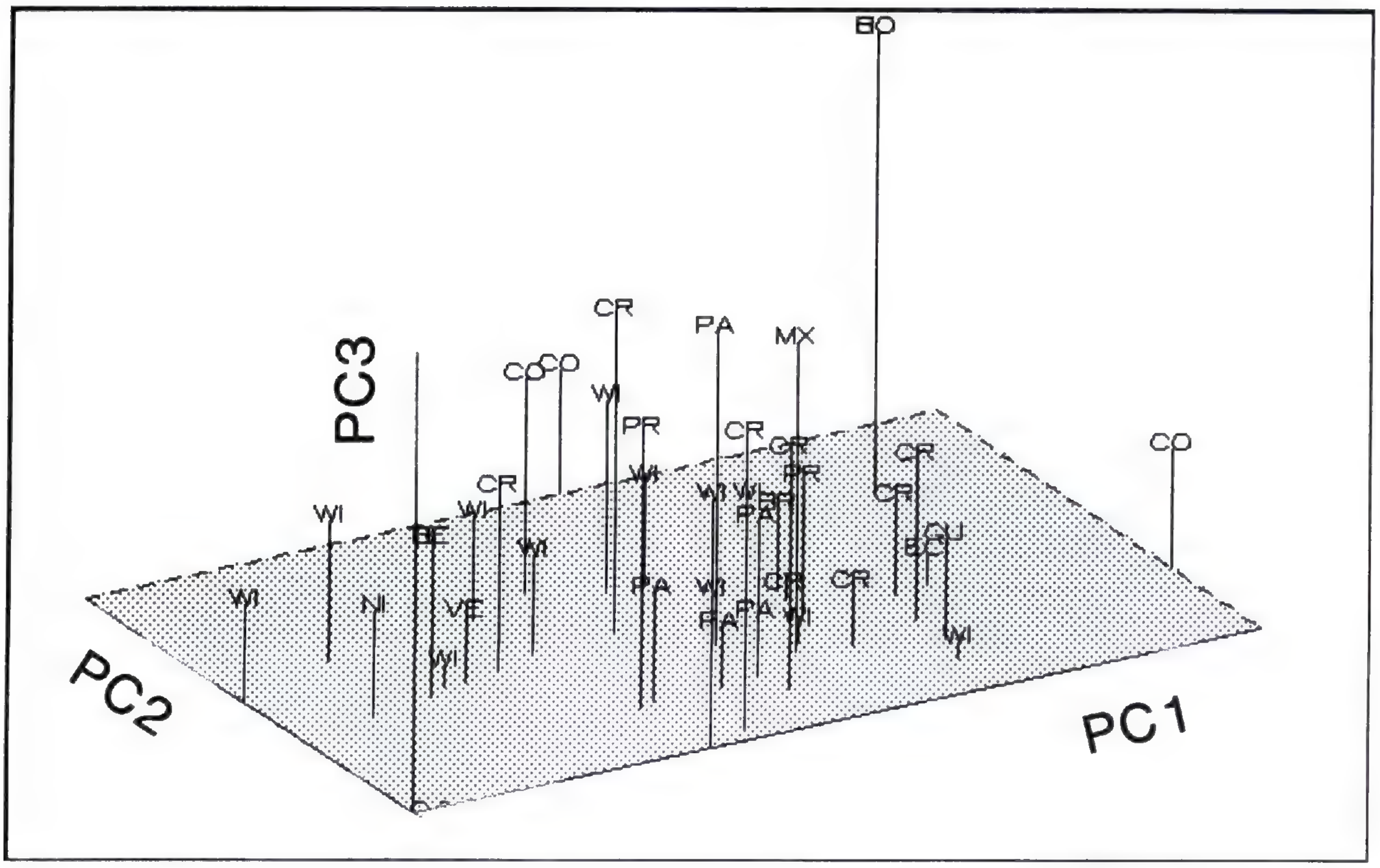



FIGURE 9. Principal Components Analysis of 30 characters of *Asplenium laetum*. BE, Belize. BR, Brazil. BO, Bolivia. CO, Colombia. CR, Costa Rica. EC, Ecuador. GU, Guatemala. NI, Nicaragua. PA, Panama. PR, Peru. VE, Venezuela. WI, West Indies.

to section *Hymenasplenium* are frequently misidentified as *A. laetum* because of their similarity in leaf cutting and outline (i.e., *A. argentinum* Hieron., *A. hostmannii* Hieron., and *A. otites* Link). These species can be distinguished from *A. laetum* by their erect rhizomes and greenish petioles. Besides these characteristics, they also differ from *A. laetum* in the form of the rachis and costa junctures. *Asplenium laetum* has the form typical of section *Hymenasplenium*: the costa is slightly sunken and bordered by a flange of green tissue that is decurrent on the adaxial surface of the rachis, and the decurrent margin of the pinna is not thickened (Fig. 16D). In contrast, the other *Asplenium* species mentioned above have prominulous costae not bordered by a flap of green tissue, and the decurrent margins of the pinnae are thickened and often a lighter color than the rest of the laminar tissue (Fig. 16C).

**4. Asplenium obtusifolium** L., Sp. Pl. 1080. 1753. *Asplenium riparium* Liebm. var. *obtusifolium* (Klotzsch & Karsten) Hook., Sp. Fil. 3: 119. 1860. TYPE: Petiver, Pter. Amer. 117, t. 2, fig. 14 (erroneously cited by Linnaeus as f. 4). [= Plumier, Traité Foug. Amér. t. 67. 1705.] Based on a plant from Morne de la Calebasse, Martinique. Figure 10; Map 5.

*Asplenium aquaticum* Klotzsch & Karsten, Linnaea 20: 354. 1847. *Asplenium obtusifolium* var. *aquaticum* (Klotzsch & Karsten) Giesenhagen, Flora 76: 172, fig. 1. 1892. TYPE: Colombia. "In locis paludosis," *Karsten s.n.* (holotype, B; photo, GH ex B).

Plants epilithic; roots 0.6–1 mm wide; rhizome 2.5–4.5 mm wide, nearly naked, the projecting apex sparsely scaly; scales 0.9–1.3 × 0.15–0.4 mm, brown, deltate-acuminate; petiole base 1.5–3.5 mm wide, swollen, 1.5–5 mm distant from each other on the same row; petiole 4–10.5 × 0.1–0.25 cm, ⅓–½ the leaf length, terete, greenish, fleshy and dull, glabrous; lamina 8–20 cm long, dark green, translucent, 1–2-pinnate (lowest pair of pinnae usually lobed or divided basally), deltate to oblong with subconform apex; rachis like petiole, narrowly marginate adaxially; lateral pinnae 2.5–4.5 × 0.8–1.5 cm in the middle of the leaf, 3–10 pairs, slightly to strongly ascending, obliquely oblong to oblong-lanceolate, often laciniate basally into 1–3 segments, simply toothed, the teeth 0.5–1.5 mm long, the basiscopic margin excavate ca. ½ the pinna length, the apex usually obtuse, rarely acute, auricle 1–2.5 mm long; veins 1-forked at middle part of pinnae; sori 4.5–9 mm long; spores papillate, 27–33 μm long for race with 64 spores per sporangium, 42–47 μm long for race with 32 spores per sporangium.

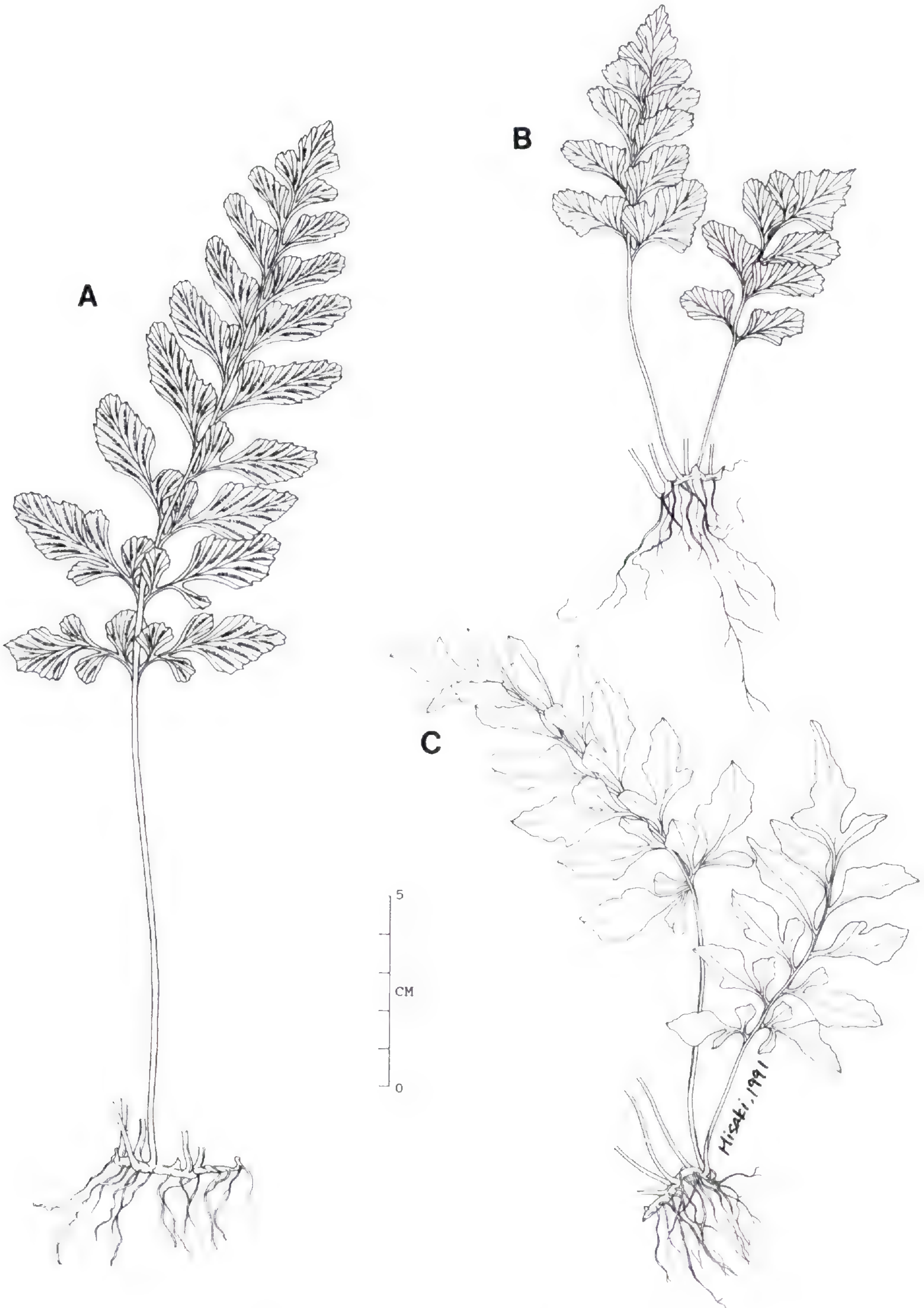
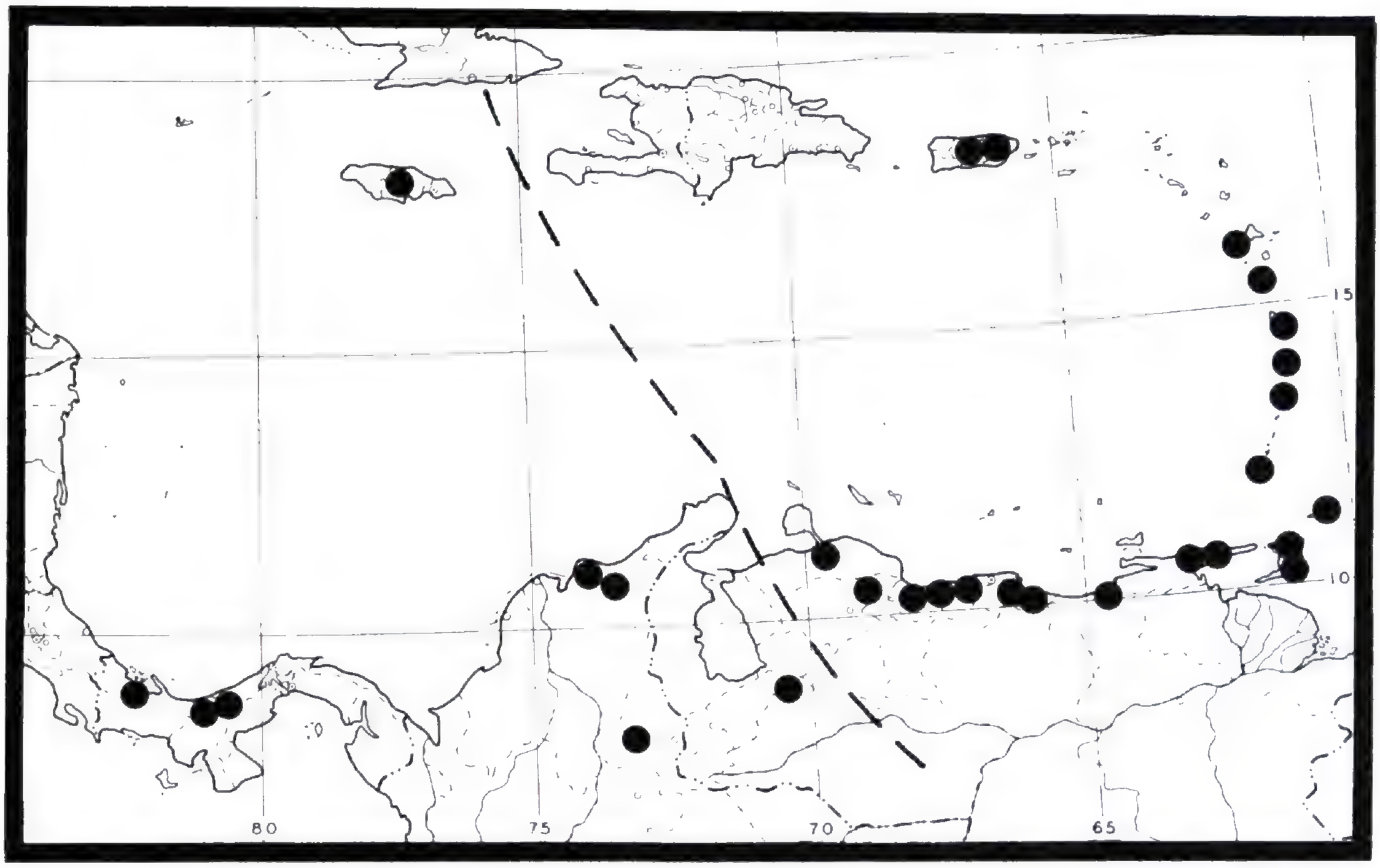



FIGURE 10. *Asplenium obtusifolium.*—A. Colombia, *H. H. Smith 1126* (NY).—B. Venezuela, *van der Werff 702* (MO).—C. Grenada, *Sherring 131* (K).

*Additional specimens examined.* PANAMA. BOCAS DEL TORO: 6.3 mi. N of bridge over Fortuna Lake, between Fortuna and Chiriquí Grande, 2.2 mi. N of Continental Divide, 820 m, 8°45′N, 82°16′W, *Croat & Grayum 60385* (AAU, MO, UC); Fortuna Dam region, along road to Chiriquí Grande, 950–1,000 m, 8°48′N, 82°10′W, *McPherson 8666* (MO). COCLE: El Copé, forest on Continental Divide above town, 700–900 m, 8°38′N, 80°38′W, *Hammel 13645* (MO, UC). VERAGUAS: vic. of Escuela Agrícola, Santa Fé, near trail to top of Cerro Tute, along stream, 800 m, *Antonio 3530* (MO); 11–13 km beyond Agricultural School at Santa Fé, valley of the Río Dos Bocas, 350–500 m, *Croat 25732* (MO); 6.5 km from Santa Fé, base of Cerro Tute, *Folsom 3062* (MO);




MAP 5. The distribution of *Asplenium obtusifolium*. The 32-spored race occurs west of the dashed line; the 64-spored race occurs east of the dashed line.

NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3964* (MO). PUERTO RICO. Toro Negro, 1936, *Quick s.n.* (MICH); prope Utuado, *Sintenis 6271* (B, BM, G, S), *6443* (B, BM, G, K, L, NY), *6533* (B, BM, G, GH, K, L, S); Toro Negro, 50 km WSW of San Juan, *Tryon 7399* (BM, GH, MO, NY). GUADELOUPE. No locality, *L'Herminier s.n.* (B, BM, GH, L, MO, NY); in 1862, *L'Herminier 79* (B, BR, G, K), *169* (L). DOMINICA. Rosalie, 1903, *Lloyd 698* (NY); Mt. Diablotin, *Lloyd 871* (NY); path from Fresh Water Lake to Boeri Lake, 800 m, *Shillingford & Adams 98* (MO); Sylvania Estate, gorge between the estate house and orange plantation, 488 m, *Hodge 1092* (GH); NE slopes of Morne Diablotin, 800 m, *Hodge & Hodge 2793* (GH), *Imray 13* (K); St. David Parish, along Boeri Lake Trail near Fresh Water Lake road, 1,200 m, *Lellinger 571* (GH); near Boeri Lake, *Whitefoord 4174* (BM); NW slopes of Morne Diablotin, *Whitefoord 4549* (BM); slopes of Micotrin, along path NW of Fresh Water Lake toward Boeri Lake, 900 m, *Wilbur et al. 7473* (F); St. Domingo, Morne Gonivo, 900 m, *Eggers 608* (B, BR, G, L, MICH, S, UC); no locality, in 1843, *Bory s.n.* (L). MARTINIQUE. Jan. 1868, *Hahn 68* (B, BM, G, GH, K, S); Calebaye, *Belanger 801* (B, G); no locality, *Duss 1636b* (F, G, GH, MO); bois des Barris-Taunes, 450–800 m, *Duss 4205* (NY); no locality, *Husnot 334* (B, BM, BR, F, G), *Pitard s.n.* (G). ST. LUCIA. Savanne Edmund District, SE of Piton Troumassée, 600–650 m, *Proctor 17703* (U); Morne Calebasse, N of Morne Rouge, 650–760 m, *Proctor 21691* (GH, U); no locality, *Sieber 363* (BM, M); in 1833, *Sieber s.n.* (BR, G); source of Canaries River, 800 m, *Box 456* (BM); Upper Roseau River, 300 m, *Box 473* (BM); St. Georges, Annandale, *Broadway s.n.* (BR, F, K, NY). ST. VINCENT. Majorca estate, 400 m, *Harrison SVT174F* (BM); Lisdara, *Hodge 2410* (GH, NY); upper valley of Richmond River, 330–540 m, *Morton 6170* (GH); without locality, *Smith & Smith 710* (BM). GRENADA. *Sherring 131* (K, NY); NW slope of Mt. St. Catherine, 500–700 m, *Proctor 17254* (GH). TOBAGO. Vil-el-Karst, main ridge, *Broadway s.n.* (BR, G, GH, MO, S); Roxborough–Parlatuvier road, near 5th milepost, 300 m, *Sandwith 1790* (BM). TRINIDAD. Maracas waterfall, *Britton et al. 1656* (GH, NY); Maracas, *Broadway 5353* (BM, BR, F, MO, UC); Maracas Falls, 200 m, *Fay 673* (K); in 1877–1880, *Fendler 139* (B, BM, G, GH, K, MO, NY, S, UC), *Hart 241* (S), *Holdridge 50* (K), *Hombersley 68* (BM); Las Cuevas, *Hombersley 390* (BM); 7 mi. N of Arima, Asa Wright Nature Centre, 400 m, *Mickel 9446* (NY). VENEZUELA. ANZOATEGUI: NE of Bergantín, Quebrada Negra, tributary of Río Zumbador, 500 m, *Steyermark 61148* (F, G, MICH, MO, NY, S); Cerro Los Pajaritos, between Cerro San José and Cerro Peonía, along headwaters of Quebrada La Tigra, 1,500–1,600 m, *Steyermark 61569* (G). ARAGUA: Henri Pittier National Park, road between Maracay and Ocumare de la Costa, 3 km N of summit, 970 m, 10°20′N, 67°34′W, *Croat 60574* (MO); prope Coloniam Tovar, *Fendler 131* (BR, G, GH, K, MO, NY); Colonia Tovar, *Moritz 384* (B, BM, BR, P, photo GH, MICH ex P); Rancho Grande, 1,000 m, *Pannier 132* (M). BARINAS: Dtto. Bolívar, entre Sto. Domingo y Altamira, en el sitio denominado Quebradón, 1,300–1,500 m, *Ortega & van der Werff 2358* (NY, UC), *Ortega & van der Werff 2348* (M). CARABOBO: arriba de Los Tanques y La Toma, entre Quebrada no. 2 y Quebrada de los Verros, en las laderas arriba de las cabeceras del Río San Gián, 750–900 m, *Steyermark & Steyermark 95249* (NY). DISTRITO FEDERAL: Depto. Libertador, entre La Peñita y Chichiriviche, a lo largo del Río Chichiriviche, 450 m, 10°31′N, 67°14′30″W, *Steyermark & Espinoza 112683* (MO, NY). FALCON: Sierra

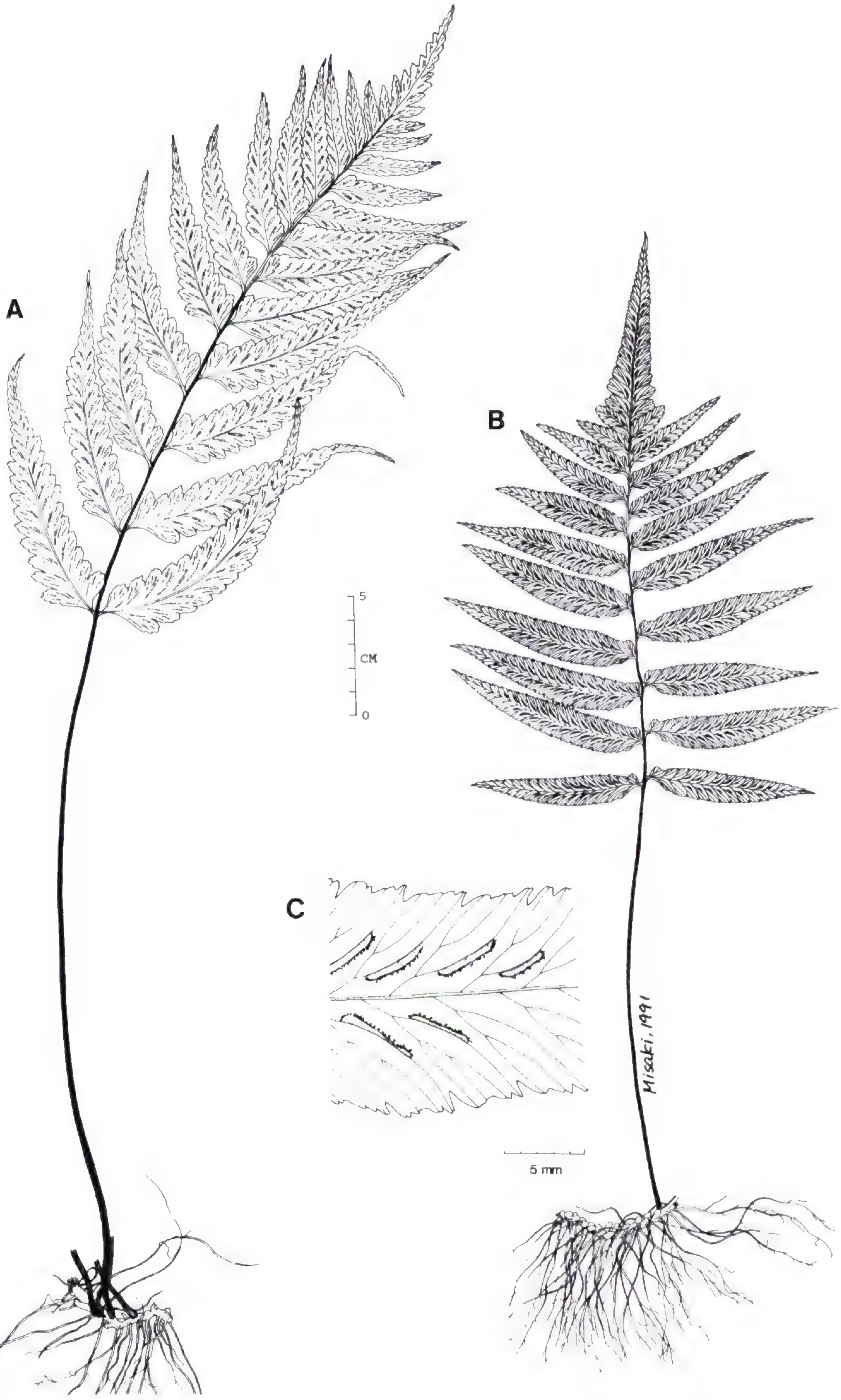



FIGURE 11.—A. *Asplenium purpurascens*, Ecuador, *Holm-Nielsen et al. 2720* (AAU).—B, C. *A. ortegae*, Venezuela, *van der Werff & González 4599* (MO).

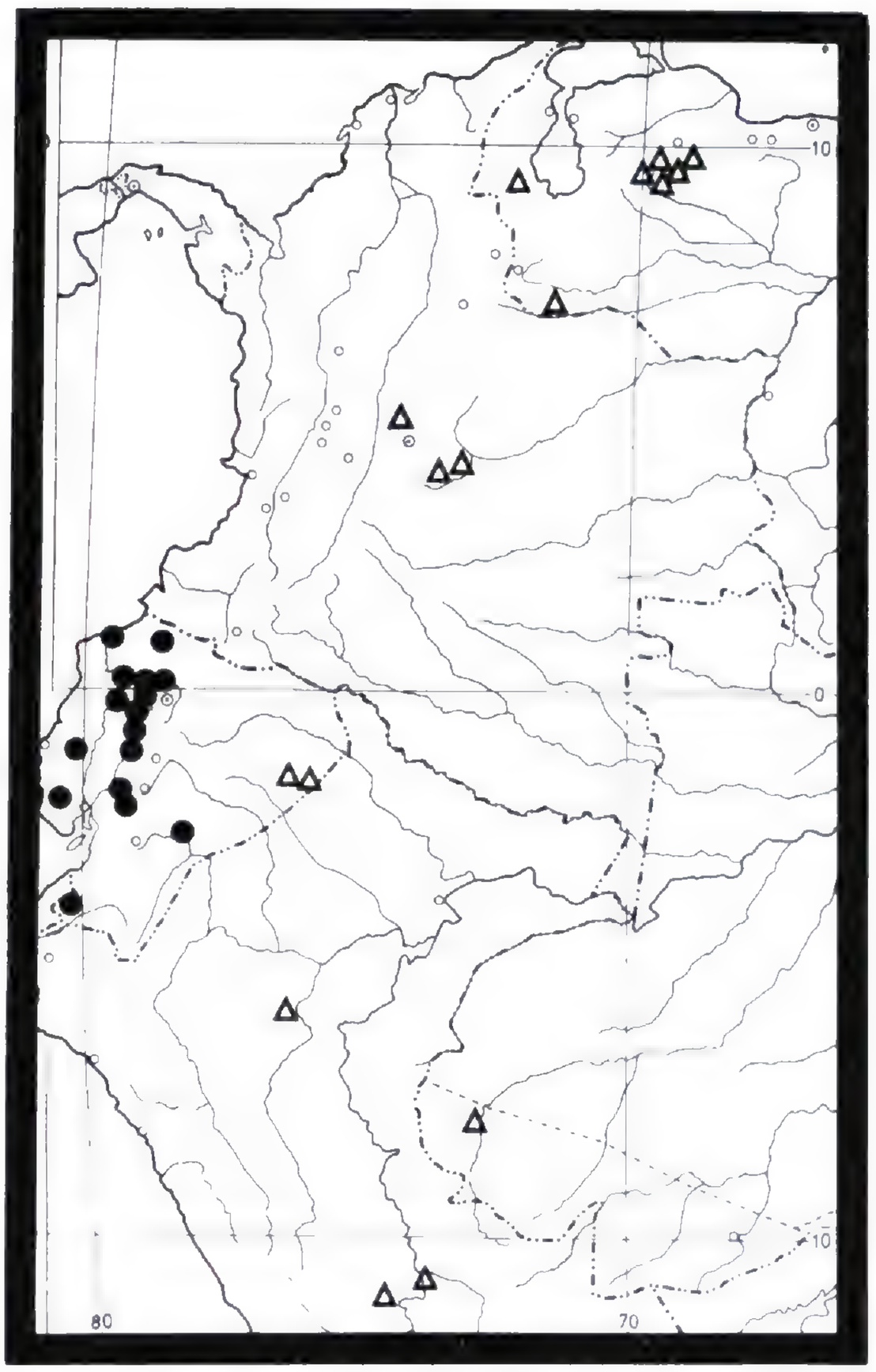
de San Luis, arriba de La Chapa, 1,200 m, *van der Werff & TR 702* (UC). LARA: area limítrofe entre Lara y Yaracuy, Dttos. Urdaneta y Bolívar respectivamente, en la Fila Azul y Hda. El Jaguar, 700–900 m, *Ortega & R. F. Smith 2440* (UC). MIRANDA: Dtto. Paéz, Fila La Tigra, Hda. San Juan, 18 km SW de Cúpira, 650 m, 10°04–05′N, 64°45′W, *Ortega & González 365* (MO, NY, UC); Cerros del Bachiller, above Quebrada Corozal, S of Sta. Cruz, 10 km W of Cúpira, 600 m, 10°9′N, 65°48′W, *Steyermark & Davidse 116896* (MO, UC). SUCRE: Península de París, Cerro de Humo, ca. 14 km N del pueblo de Río Grande Arriba, arriba de Boca de Cumaná y Punto Siparo, NE de Irapa, 1,060 m, *Steyermark 94822* (NY); Península de Paria, Cerro de Río Arriba, W de Cerro de Humo, a lo largo de Río Santa Isabel, arriba de Santa Isabel, 600–700 m, *Steyermark & Rabe 96232* (NY); Dtto. Cagigal, Península de Paria, near border with Dtto. Arismendi, low trail between El Paujil and El Brasil, 850–890 m, 10°39–40′N, 62°43′W, *Steyermark et al. 121451* (MO, NY, UC); Dtto. Arismendi, Península de Paria, between Tacarigua and Río Tacarigua, E of Cerro de Humo, 560 m, 10°41–42′N, 62°36–37′W, *Steyermark et al. 121590* (MO, UC). COLOMBIA. PROV. UNKNOWN: *Karsten s.n.* (B). MAGDELENA: Sierra Nevada de Santa Marta, Alto Río Buritaca, Alto de Mira, 900–1,100 m, *Madriñán & Barbosa 258* (GH, MO); Sierra Nevada de Santa Marta, edge of Quebrada La Sirena, 1,100 m, 10°59′N, 73°59′W, *Kirkbride 2188* (COL, NY, UC); Santa Marta, above Onaca, 1,100 m, *H. H. Smith 1126* (B, BM, BR, COL, G, GH, L, MICH, MO, NY, S, UC). NORTE DE SANTANDER: Ocaña, 1,600 m, *Schlim 653* (B, BR, G, K, L). SANTANDER: Tequendame, 1,200 m, *Kalbreyer 951b* (B).

*Asplenium obtusifolium* has a circum-Caribbean distribution (Map 5). It grows in the spray of, or underneath, waterfalls and on wet rocks along shaded streams. Its elevational range is 200 to 1,200 m.

This species is characterized by greenish petioles, fleshy leaves, small (8–20-cm-long) laminae, and few (3–10) pinna pairs. The pinnae are usually obtuse and the basal pairs lobed or divided basally (Fig. 10).

*Asplenium obtusifolium* is remarkable by having two races: one with 32 spores per sporangium, the other with 64 spores. The sporophytes of the two races appear indistinguishable and could not be distinguished by a Principal Component Analysis of 20 quantitative morphological characters (Fig. 5). The two spore races differ geographically, with the 32-spored race occurring only in the western portion of the range and the 64-spored race occurring only in the eastern portion (Map 5).

The 32-spored race is presumably apogamous, but this idea needs to be investigated. In the Old World, *A. apogamum* Murakami & Hatanaka, *A. cheilosorum* Kunze, and *A. hondoense* Murakami & Hatanaka have been shown to have both a sexual race with 64 spores per sporangium and an apogamous race with 32 spores per sporangium (Mitui et al., 1989). Therefore, it seems likely that the 32-spored race of *A. obtusifolium* is apogamous.




MAP 6. The distribution of *Asplenium purpurascens* (solid dots) and *A. ortegae* (open triangles).

**5. Asplenium ortegae** Murakami & R. C. Moran, sp. nov. TYPE: Venezuela. Apure: Dtto. Paéz, along Río Arauca at Colombian border, *van der Werff & González 4599* (holotype, MO; isotype, NY). Figure 11B, C; Map 6.

Plantae terrestres. Rhizoma 3.5–5.2 mm latum, internodiis approximatis, squamis 0.5–1.9 mm longis, ca. 0.2 mm latis, lanceolatis, clathratis, brunneis vel nigriscentibus, 3–6-cellulas latis. Petioli 6–21 cm longi, atrobrunnei, nitidi, sparse squamulosi; laminae 11–25 cm longae, 9–18 cm latae, deltatae vel late oblongae, ad apicem abrupte angustatae, segmento terminali lobato, elongato; pinnae plerumque 4.5–9 cm longae, 1.1–1.7 cm latae (pinnae basales interdum profunde lobatae et usque ad 3 cm latae), 6–10-jugatae, breviter petiolatae vel sessiles, latere acroscopico basali truncato, rotundato vel (in Amazonia occidentali) cuneato, nunquam auriculato, latere basiscopico basali cuneato vel excavato, marginibus typice serratis vel serrate lobulatis, interdum in foliis maximis usque ad costas, apice longe attenuatis. Rhachis basaliter atrobrunnea vel nitida, distaliter viridula, infra sparse squamulosa vel glabrata. Venae (2 )3–4-furcatae. Sori 3–7 mm longi.

Plants terrestrial; roots 1.1–1.7 mm wide; rhizome 3.5–5.2 mm wide, nearly naked; scales 0.5–1.9 × 0.23–0.29 mm, black-brown, lanceolate; petiole base 2.2–5.5 mm wide, swollen, 0.5–1.1 mm distant from each other on the same row; petiole 6–21 × 0.09–0.15 cm, ⅓–½ the leaf length, atropurpureous, sparsely scaly at base; lamina 11–25 cm long, light green, herbaceous, 1-pinnate, deltate to oblong with acuminate apex, apex pinnatifid, abruptly reduced or evenly tapered; rachis green to dark reddish purple, grooved with green herbaceous wings perpendicular to the plane of the lamina; lateral pinnae 5–9 × 0.9–1.7 cm in the middle of the leaf, 6–10 pairs, lanceolate to linear-lanceolate, the margin slightly double-toothed, 0.5–1.3 mm deep, the basiscopic side excavate for 1/10–1/5 the length of the pinnae, stalked at lower pinnae, auricle absent; veins 3–4 times forked; sori 3–7 mm long; spores about 30 μm, 64 per sporangium, perispore cristate.

*Paratypes.* VENEZUELA. PORTUGUESA: Dtto. Ospino, Quebrada Honda, en el caserio La Cristobera, *Ortega et al. 3093* (BM); Dtto. Guanare, Mpio. Papelón, rivera izquierda del caño Iguez, *Pérez 1* (UC); Dtto. Guanare, terrenos del la UNELLEZ, una quebrada en la Mesa Alta, 9°4′N, 69°49′W, *Ortega 1912* (UC); Dtto. Araure, en los Ríos Bocoy y Riecito, límite entre los Estados Lara y Portuguesa, 800–1,200 m, 9°37′N, 69°25′W, *Ortega & Aymard 1817* (UC); entre Agua Blanca y Los Hijitos, 160 m, *Ortega & Aymard 2087* (NY); entre Agua Blanca y San Rafael, Quebrada Los Hijitos, 160 m, *Ortega & Aymard 2088* (UC); Dtto. Guanare, along road to San José de La Montaña, 500 m, 9°20′N, 69°43′W, *A. R. Smith et al. 1062* (UC); Boca de Monte, 23 km N del vado del Río Suruguapo, 38 km N por la autopista Guanare–Ospino, en sitio Las Marías, 400 m, 9°18′N, 69°43′W, *Steyermark et al. 127134* (MO, UC). ZULIA: Dtto. Perijá, 2 km W of the intersection of the Río Aricuaisá and the Maracaibo–La Fría Hwy. (Hwy. 6), 10 m, *Davidse et al. 18205* (MO, UC); Dtto. Colón, intersection of Río Catatumbo and La Fría–Maracaibo Hwy. (Hwy. 6), 30 m, 9°07′N, 72°37′W, *Davidse et al. 18826* (MO, UC); Dtto. Colón, intersection of Río Catatumbo and the La Fría–Maracaibo Hwy. (Hwy. 16), 30 m, *Davidse et al. 18826* (MO, UC); Boca de Monte, 23 km N del vado del Río Suruguapo, 38 km N por la autopista Guanare–Ospino, en el sitio Las Marías, 400 m, *Steyermark et al. 127131* (MO, UC). COLOMBIA. CUNDINAMARCA: Carretera Medina desviación a la izquierda, Río Humea, 500–550 m, *Murillo 2197* (MO). META: Río Guatiquia, *Lehmann 8830* (B); Puerto López, 240 m, *Little & Little 8427* (COL). ECUADOR. PASTAZA: Lorocachi, 2 km upriver on Río Curaray, opposite Military Camp, 200 m, 1°28′S, 75°58′W, *Brandbyge & Asanza C. 31225* (AAU); Ceilán, Pica from Ceilán to Río Cononaco, on the N side of Río Curaray, 200 m, 1°36′S, 75°40′W, *Brandbyge & Asanza C. 31649* (AAU, F, UC). PERU. JUNIN: Colonia Perene, 680 m, *Killip & Smith 24924* (F); Puerto Bermúdez, 375 m, *Killip & Smith 26633* (F). LORETO: Yurimaguas, lower Río Huallaga, 135 m, *Killip & Smith 29078* (NY). BRAZIL. ACRE: Cruzeiro do Sul, Rio Juruá and Rio Moa, between Mundurucus and Tatajuba, Rio Juruá, *Maas et al. P12902* (F).

*Asplenium ortegae* is named for Francisco Ortega, prominent Venezuelan pteridologist, who has given us much hospitality and assistance during fieldwork in Venezuela.

From Colombia to Bolivia, the species occurs on the eastern side of the Andes; in Venezuela, it occurs on both sides (Map 6). It grows on shaded forest floors in wet forests from 0 to 500(–800) m.

*Asplenium ortegae* is characterized by short-creeping rhizomes, atropurpureous petioles, truncately serrate-lobed pinna margins, and usually 3- or 4-forked veins (Fig. 11B, C). Rarely, the basal pinnae become pinnatifid, and the plants then resemble *A. purpurascens* (which also has atropurpureous petioles). The two species may be separated by the characteristics given in the key.

Despite the resemblance to *A. purpurascens*, evidence from chloroplast DNA supports a close relationship of *A. ortegae* with *A. delitescens* (this evidence will be presented in a future paper by the first author). Morphological characteristics also support this relationship. Both species have deltate laminae, relatively few (6–10) pinna pairs, and similarly shaped laminar apices. *Asplenium delitescens*, however, differs by having stramineous petioles, less serrate pinna margins, and twice-forked veins (Fig. 6A). It may eventually be shown that *A. ortegae* is of hybrid origin involving *A. delitescens* as one of its parents.

**6. Asplenium purpurascens** Mett. ex Kuhn, Linnaea 36: 102. 1869. TYPE: Ecuador. Chimborazo: "ad pedem montis Chimborazo," *Spruce 5697* (holotype, B not seen; fragment, B). Figure 11A; Map 6.

*Asplenium melanopus* Sodiro, Anal. Univ. Quito 9: 88. 1893 [= Crypt. Vasc. Quit. 189. 1897]. *Diplazium melanopus* (Sodiro) Hieron., Bot. Jahrb. Syst. 34: 456. 1904. SYNTYPES: Ecuador. Pichincha: "Crece en la región tropical, en los bosques de los Colorados," *Sodiro s.n.* (isosyntype, K); "en el valle de Pallatanga cerca de Puente de Chimbo," *Sodiro s.n.* (isosyntype, K).

Plants terrestrial; roots 1.5–2 mm wide; rhizome 4.2–6.5 mm wide, sparsely scaly; scales 1.6–2.3 × 0.35–0.55 mm, black to dark brown, lanceolate; petiole base 2–5 mm wide, swollen, 2–4 mm distant from each other on the same row; petiole 17–27 × 0.15–0.2 cm, about ½ the leaf length, dark reddish purple, scaly at base; lamina 20–30 cm long, dark green, firm-herbaceous, 1-pinnate, deltate, the apex attenuate, pinnatifid; rachis like the

petiole, grooved, with herbaceous green wings; lateral pinnae 6.5–12 × 1.3–2.5 cm in the middle of the leaf, 8–11 pairs, lanceolate to linear-lanceolate, long-acuminate, the basiscopic side excavate for ⅐–⅕ the length of the pinna, stalked at the lower pinnae, auricle absent, the margin lobed to pinnatifid, the tip of each lobe with rounded teeth, about 1 mm deep; veins 3–4 times forked; sori 4–8 mm long, often diplazioid; spores 27–33 μm, 64 per sporangium, perispore cristate.

*Additional specimens examined.* ECUADOR. CHIMBORAZO: vic. of Sacramento, on E side of Río Sacramento, 1,200–2,000 m, *Wiggins 11095* (NY, UC). COTOPAXI: Tenefuerste, Río Pilalo, km 52–53, Quevedo–Latacunga, 750–1,300 m, *Dodson & Gentry 12275* (MO, QCNE); 20 km NW of Corazón, Río Guapara, 250 m, *Sparre 17173* (S); in confiano Columbiae, *Buchwald 43* (UC); El Recreo, *Eggers 15214* (B, BM, L). ESMERALDAS: near San Mateo, road to Esmeraldas airport, gravel road 8.6 km beyond bridge over Río Esmeraldas, ca. 6.6 km beyond Univ. Luis Vargas Torres Est. Exp. Mutile, along Río Mutile, 80 m, 0°52′N, 79°33′W, *Croat 55622* (F, MO, UC). GUAYAS: near Bucay, western cordillera, junction of the provinces of Guayas, Canar, Chimborazo, and Bolívar, 300–400 m, *Camp 3785* (F, GH, NY); Loma Alta, Cerro de Vacas Muertas, Cordillera de Colonche, 250 m, *Valverde 510* (MO). LOJA: W of El Limo, Alamor–Cazaderos Road, 1,400 m, *Harling & Andersson 22310* (F). LOS RIOS: Río Palenque Biological Station, km 56 Rd. Quevedo–Sto. Domingo, 150–220 m, *Dodson & Gentry 10051* (MO, QCNE); ca. 40 km E of Babahoyo, surroundings of Montalvo, 100–200 m, 1°47′S, 79°17′W, 2,720 m, *Holm-Nielsen et al. 2720* (F, MO); near Montalvo, ca. 40 km E of Babahoyo, foothills of the Andes, 100–200 m, 1°47′S, 79°17′W, *Holm-Nielsen et al. 2720* (AAU, B). MANABI: 11 km E of San Plácido, on road Portoviejo–Pichincha, 400 m, *Harling & Andersson 24978* (F). PICHINCHA: Km 170–175, via Sto. Domingo–Quinindó, 300 m, *Acosta S. 13815* (F); Reserva ENDESA, Carretera Quito–Puerto Quito, km 113, 00°05′N, 79°02′W, *Argüello 498* (AAU); Reserva ENDESA, Carretera Quito–Puerto Quito, km 113, 800 m, 00°05′N, 79°02′W, *Ayala 58* (AAU); San José de Toachi, 100 km W of Quito, 1,000 m, *Bell 200* (BM, GH, S); by Río Toachi, above confluence with Río Pilaton, 1,000 m, *Bell 238* (BM, GH, S); 20 km W of Sto. Domingo de los Colorados, 300 m, *Cazalet & Pennington 5199* (B, K, UC); 20 km W of Sto. Domingo de los Colorados, 300 m, *Cazalet & Pennington 5224* (UC); Sto. Domingo de los Colorados, *Fagerlind & Wibom 1593* (S); Sto. Domingo de los Colorados, 500 m, *Holdridge 1617* (GH); Finca Carlita, at km 13 on road to Sto. Domingo, 550 m, 00°15′S, 79°14′W, *Holm-Nielsen et al. 7066* (AAU); valle Nanegal, Aug. 1874, *Sodiro 8.74* (K); prope Sto. Domingo, Aug. 1875, *Sodiro 8.75* (K).

*Asplenium purpurascens* is largely restricted to the western side of the Andes of Ecuador (Map 6). It grows in wet forests from 80 to 1,400 m.

The species is characterized by short-creeping rhizomes, atropurpureous petioles and rachises, and pinnatifid pinnae (Fig. 11A). No other neotropical species of section *Hymenasplenium* has regularly pinnatifid pinnae.

The holotype of *A. purpurascens* was not among the specimens we received on loan from B. There were two very small fragments on a sheet at B, but these were not enough to identify the species. We feel confident that we are applying the name correctly because it is possible to distinguish the species based on Mettenius's original description. According to his description, *A. purpurascens* has creeping rhizomes, lustrous purple petioles, and pinnatisect pinnae. The provenance of the type also agrees with applying the name to the above-cited plants.

**7. Asplenium repandulum** Kunze, Linnaea 9: 65. 1834. TYPE: Peru. Huánuco: Pampayaco, in sylvis montosis ad arborum truncos, July 1829, *Poeppig s.n.* (holotype, B not seen; isotype, NY (fragment) not seen). Figure 12; Map 7.

Plants epiphytic; roots 0.6–1.5 mm wide; rhizome 2.5–7 mm wide, nearly naked; scales 0.5–2.5 × 0.2–0.5 mm, black, ovate-lanceolate, clathrate; petiole base 2.5–4 mm wide, swollen, 1–2 cm distant from each other on the same row; petiole 4–15 × 0.15–0.3 cm, about ⅐–⅓ the leaf length, dark green-brown, fleshy and dull, terete, glabrous; lamina 22–40 cm long, dull green, 1-pinnate, lanceolate to oblong with subconform apex; rachis like petiole, with adaxial green wings in the same plane as the lamina, strongly carinate abaxially; lateral pinnae 4–6 × 1.1–1.8 cm in the middle of the leaf, 12–17 pairs, obliquely oblong to oblong-lanceolate, margin almost entire to only slightly toothed, the basal basiscopic side excavate for ⅐–¼ the pinna length, acute at apex, broadly cuneate and almost sessile at base, auricle 2–6 mm long; veins 1-forked; sori 4–10 mm long; spores 40–48 μm, 64 per sporangium, spiny.

*Additional specimens examined.* ECUADOR. MORONA-SANTIAGO: Macuma, on the Macuma River, S of Chiquaza, 700 m, *van der Werff 660* (GH, MO). PASTAZA: Baños—aut Jivaria de Pintuc, excurs. nach Canelos, 1,200–1,300 m, *Stübel 878* (B). PICHINCHA: prope Sto. Domingo, Aug. 1875, *Sodiro s.n.* (K). PERU. AMAZONAS: ca. 12 km E of La Peca, Serranía de Bagua, 1,650–1,800 m, *Gentry et al. 23073* (MO, UC). HUANUCO: Leoncio Prado, Dtto. Hermilio Valdizan, road from Pumaguasi to La Cumbre, La Divisoria, 1,600 m, *Plowman & Schunke V. 7363* (F). JUNIN: Chanchamayo, Chanchamayo Valley, 1924–1927, *C. Schunke 155* (F), *897* (F), *907* (F); above San Ramón, Schunke Hacienda, 1,400–1,700 m, *Killip & Smith 24547* (NY), *24804* (NY); Pichita Caluga, 1,800 m, *Walden 41* (BM); Tarma, Chanchamayo Valley, above La Merced at Cumbre Yacunay

FIGURE 12. *Asplenium repandulum*. A, B. Ecuador, *van der Werff 660* (MO). Cross section of rachis shown in A.—C. Peru, *Hutchison 1196* (G).

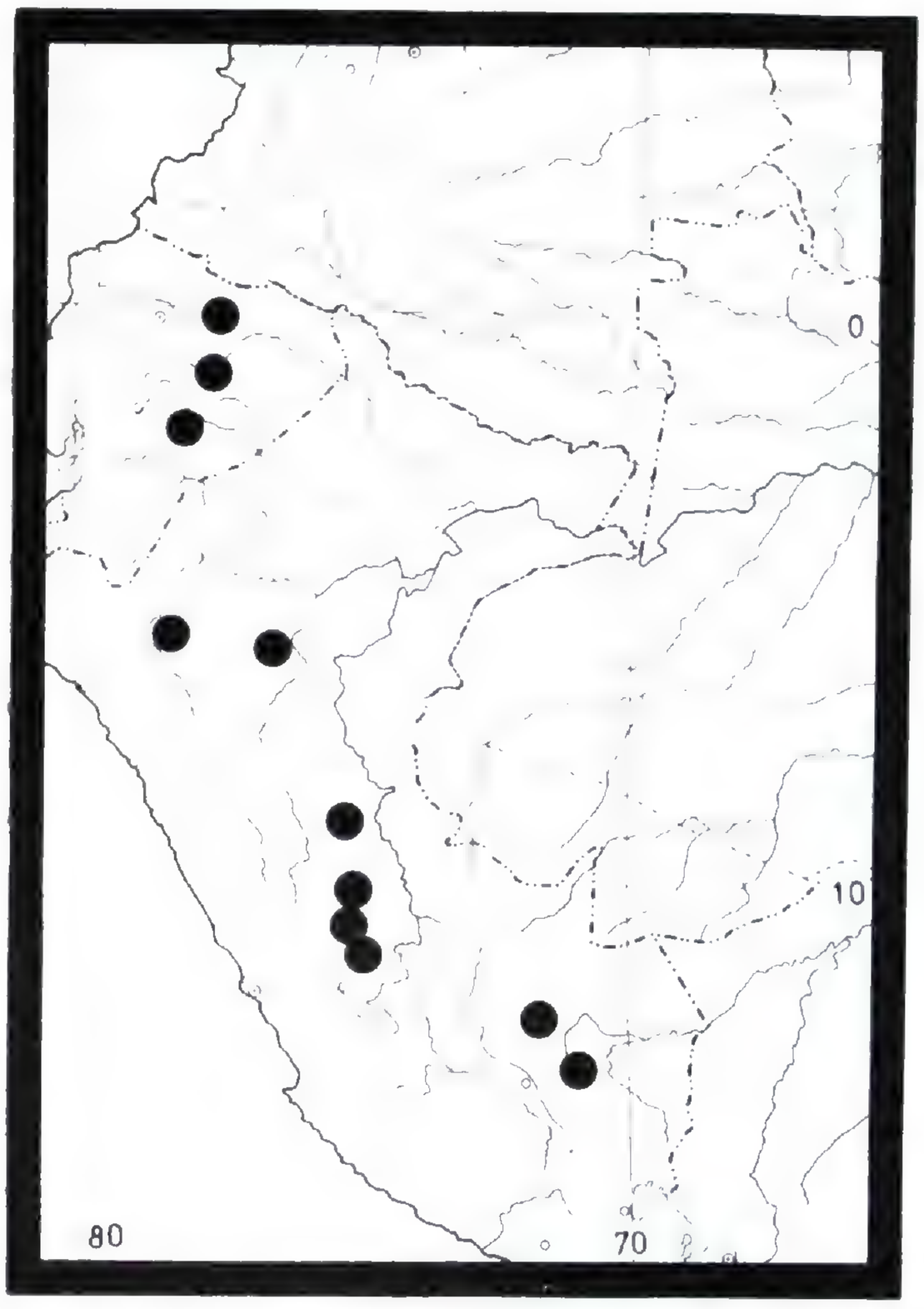
near summit, 2,000 m, *Hutchison 1196* (F, G, M, MICH, MO, NY, S). MADRE DE DIOS: Manú, Parque Nacional de Manú, between Panagua and Tayakome, Cocha Cashu, vicinity of ox-bow lake of Río Manú, *Foster et al. 3449* (F); reise von Moyabomba zum Huallaga, bei Lamas, *Stübel 1099a* (B). PASCO: Oxapampa, vic. of Chequitavo, Gran Pajonal, 1,250 m, 10°45′S, 74°23′W, *D. N. Smith 5168* (MO).

*Asplenium repandulum* is characterized by long-creeping rhizomes, prominently carinate rachises, and orientation of the rachidial wings in the same plane as the lamina (Fig. 12). It occurs east of the Andes in Ecuador and Peru (Map 7). It grows in wet forests from 700 to 2,000 m as an epiphyte on large tree trunks. One specimen from French Guiana, disjunct from the Andean populations, has a carinate rachis and may represent *A. repandulum* but was collected on wet soil (Sommet Tabulaire, ca. 50 km SE of Saul, 750 m, *de Granville 3508* (F)). In the carinate rachis, it also resembles *A. triquetrum*, but the main range of that species is even farther away than that of *A. repandulum*. It is not typical of either species to grow on the soil. The identity of the plant from French Guiana needs more research.

As outlined in the key, the rachis cross section and orientation of the adaxial wings on the rachis are important taxonomic characteristics distinguishing *A. repandulum*, *A. triquetrum*, *A. riparium*, and *A. volubile*. The characteristics, however, can be difficult to interpret because of changes during pressing and drying. Although the carinate rachis of *A. repandulum* and *A. triquetrum* is a prominent and striking feature of living plants, in pressed plants the keeled edge of the rachis is pushed to one side, so that only one side of the 3-angled rachis faces up. This gives the impression when viewed from above that the rachis is smooth or rounded. When this distortion occurs, it can usually be detected because pinna bases on one side of the rachis are hidden beneath the keel, but the attachments of the pinna bases on the other side are visible.

The orientation of the rachidial wings may be difficult to determine because the wings sometimes shrivel upon drying and (in *A. riparium* and *A. volubile*) the wings may be pressed flat into the same plane of the lamina. Usually, the best place to observe the orientation of the wings is at the pinna junctures.

*Asplenium repandulum* is most closely related to *A. triquetrum* based on rachidial wing orientation and the strongly carinate rachis. However, *A. repandulum* resembles *A. volubile* by the long-creeping rhizomes and epiphytic habit (see *A. volubile* for comparison).




MAP 7. The distribution of *Asplenium repandulum*.

Although we have not seen the holotype of *A. repandulum*, we feel confident that we are applying the name correctly because this is the only epiphytic species of section *Hymenasplenium* that occurs in Amazonian Peru.

**8. Asplenium riparium** Liebm., Mexic. bregn. 244 (seors. 92). 1849. [= Kongel. Danske Vidensk. Selsk. Skr., Naturvidensk Afd., ser. 5, 1: 244. 1849]. *Asplenium obtusifolium* L. var. *riparium* (Liebm.) Domin, Pteridophyta Isl. Dominica in Rozpr. Král. Ceské Spolecn. Nauk, Tr. Mat.-Prir., Nov. Rad. 2: 175. 1929. LECTOTYPE (designated by A. R. Smith, 1981): Mexico. Veracruz: Hacienda de Java, *Liebmann* [Fl. Mex. 310] (lectotype, C not seen; isolectotypes, B, K). Figure 13B; Map 8.

Plants epilithic or terrestrial; roots 0.7–1.3 mm wide; rhizome 3–6 mm wide, nearly naked; scales 0.8–1.5 × 0.2–0.4 mm, brown, ovate-lanceolate; petiole base 2.5–4.5 mm wide, swollen, 1–2.5 mm distant from each other on the same row; petiole 10–20 × 0.1–0.25 cm, ⅓–½ the leaf length, dark green-brown, fleshy and dull, broadly and shallowly grooved, glabrous; lamina 15–30 cm long, dark green, 1(–2)-pinnate, lanceolate with conform

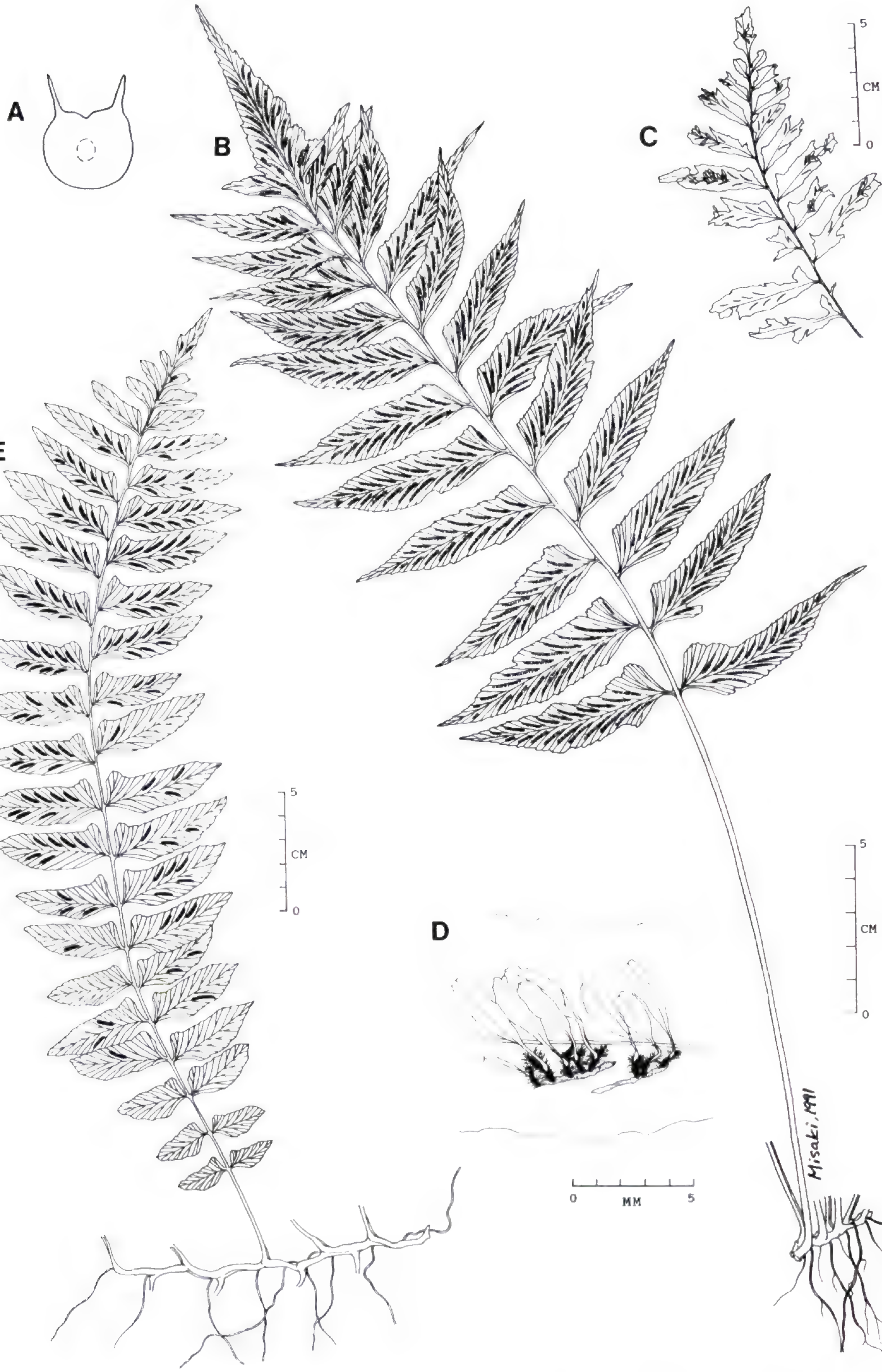



FIGURE 13. A–D. *A. riparium.*—A. Cross section of rachis.—B. Fertile leaf, Colombia, *H. H. Smith 968* (MO).—C. Senescent leaf with plantlets, *Murakami s.n.* (MO).—D. Plantlets proliferating from receptacular tissue of senesced leaf.—E. *Asplenium volubile*, Ecuador, *Asplund 5550* (F).

terminal pinna, herbaceous; rachis like petiole, with green wings perpendicular to the plane of the lamina; lateral pinnae 4–8 × 1–2 cm in the middle of the leaf, 8–14 pairs, oblong-lanceolate, the margin toothed, the teeth about 0.5 mm deep, the basiscopic margin excavate for ⅙–⅓ the pinna length, broadly cuneate and almost sessile at base, auricle 1–4 mm long; veins 1–3 times forked; sori 5.5–10 mm long; spores 38–43 μm, 64 per sporangium, spiny. $n = 39$ or 40 (Smith & Mickel, 1977).

MAP 8. The distribution of *Asplenium riparium*.

*Additional specimens examined.* MEXICO. CHIAPAS: Mpio. of Rayón, in the Selva Negra 10 km above Rayón Mezcalapa along road to Jitotol, 1,700 m, *Breedlove 26082* (F, MICH, MO, NY), *29819* (F, MICH, NY), *32617* (MICH, NY); Mpio. of Rayón, above Rayón Mezcalapa along road to Jitotol, 1,700 m, *Breedlove 35410* (MO); Mpio. of Cintalapa, 3 km E of Francisco Madero, NE of Cintalapa, 1,250 m, *Breedlove 38081* (MO); 2 mi. N of Colonia Toquian, on S slope of Volcán Tacaná, 1,700 m, *Croat 47151* (MO); in 1864–1870, *Ghiesbreght 416* (K); 11.6 mi. N of Linda Vista Tropical Biol. Sta., Pueblo Nuevo Solistahuacán, *Gittins 4220* (NY); Siltepec, *Matuda 221* (MICH, MO); *Bourgeau 362* (B). OAXACA: Dtto. Villa Alta, from Yetzelalag toward Lovani, 1,200 m, *Hallberg 1498* (NY); Dtto. Tehuantepec, between La Chiguzhe and Guevea de Humboldt, along Continental Divide, 1,100–1,500 m, *Hallberg 1744* (NY, UC); Mpio. Sta. María Chimalapa, ca. 7 km S de Sta. María, por la vereda a la cabecera del Río Escolapa, 400 m, 16°51′N, 94°41′W, *Hernández G. 2457* (NY); ca. 15 km al ESE de Sta. María, filo entre Arroyo Majipana (al O) y Río Blanco (al E), 810 m, 16°52′N, 94°34′30″W, *Hernández G. 2523* (NY); Mpio. Sta. María Chimalapa, ca. 8 km al N de Sta. María, cañada al O de la vereda al paso Jugcuypac del Río Verde, 300 m, 16°57′N, 94°41′W, *Hernández G. & González L. 1749* (MO, NY); 24 km S of Valle Nacional (km 85), road from Ixtlán to Tuxtepec, 900 m, *Mickel 1434* (MICH, NY); Dtto. Ixtlán, 79 km W of Ixtlán de Juárez on Rte. 175, 1 km S of Campamento Vista Hermosa, 1,500 m, *Mickel 5650* (NY, UC); Dtto. Tuxtepec, 4–9 km S of Valle Nacional on Rte. 175, 300–700 m, *Mickel 5893* (UC); 200–700 m, *Mickel 5918* (NY, UC); Dtto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, 500–700 m, *Mickel 6360* (NY, UC); Dtto. Ixtlán, 29 km S of Valle Nacional, 80 km N of Ixtlán de Juárez, trail E of Rte. 175 at Campamento Vista Hermosa toward Ladú, 500 m, *Mickel 6446* (NY); Dtto. Ixtlán, 7 km S of Vista Hermosa, 71 km N of Ixtlán de Juárez on Rte. 175, 1,800 m, *Mickel 6715* (NY, UC); Dtto. Ixtlán, 2 3 km S of Vista Hermosa, 75–76 km N of Ixtlán de Juárez on Rte. 175, 1,400 m, *Mickel & Pardue 6548* (AAU, NY); Dtto. Ixtlán, 2–3 km S of Vista Hermosa, 75–76 km N of Ixtlán de Juárez on Rte. 175, 1,700 m, *Mickel & Pardue 6580* (UC); Ixtlán, 76 km N of Ixtlán de Juárez on Rte. 175, Campamento La Esperanza, *Mickel 7172* (Z); Villa Alta, ca. 20 mi. NE of Villa Alta, valley of the Yelagago River, 1,200 m, 17°25′N, 96°05′W, *Mickel 1087* (MICH). PUEBLA: Curva de los Millones, 10 km E de Teziutlán, *Riba et al. 318* (NY). VERACRUZ: 8 km S of Misantla, 750 km, *Barrington 404* (GH); 12 km S of Misantla, 1,350 m, *Bohs et al. 1701* (GH); 15 km S of Misantla, Paz de Enriquez cloud forest, *Bohs et al. 1832* (GH); vallée de Córdoba, *Bourgeau 2014* (B, GH, K, L, MICH, MO, NY); 8 km S of Misantla, 750 m, *Conant 700* (GH); in 1889–1891, *Finck 35* (NY); Mirador, *Galeotti 6274* (BR, K), *6275* (photo GH ex BR), *Linden 31* (MICH); Sta. Rita prope Misantla, *Hahn 362* (K); 12 km S of Misantla, 1,350 m, *Kress et al. 703* (GH); Barranca de Mirador, *Liebmann s.n.* (B, K); Mirador, in 1839, *Linden 68* (K); Orizaba, in 1835, *Müller 1772* (NY); 7.2 km E of Tebanca, 7.2 km E of E side of Lago Catemaco, 2.6 km W of Bastonal lumber camp, 910 m, *Nee & Schatz 19943* (F); Barranca of Texolo, near Jalapa, 1,100 m, *Pringle 7889* (GH); Zacuapan, *Purpus 1983* (B, UC); Barranca de Tenampa, *Purpus 2846* (B, BM, F, GH, MO), *Purpus 2946* (M), *Purpus 15420* (F); environs of Xalapa, road from Xalapa to Misantla, Paz de Enriquez, N of Naolinco, 1,600 m, *Sperling 4945* (GH); below Sta. Rita, 12 km S of Misantla, 1,350 m, *Sperling 4995* (GH); Mpio. Yecuatla, Loma Santa Rita, 1,300 m, *Ventura A. 3267* (NY); Mpio. de Atzalan, Ranchito El Caballo, 1,000 m, *Ventura A. 14368* (G); Mpio. Totutla, El Mirador, 1,000 m, *Ventura A. 16002* (MO). GUATEMALA. ALTA VERAPAZ: trail between Sepacuite and Secanquim, 1,000 m, *Maxon & Hay 3263* (BM, F, NY); E of Tactic, on road to Tamahú, 1,500–1,650 m, *Standley 71321* (F); road between Tactic and the divide on road to Tamahú, 1,500–1,600 m, *Standley 90658* (F); between Tactic and the divide to Tamahú, 1,500–1,600 m, *Standley 90667* (F, UC); Pansamalá, 1,200 m, *von Türckheim 630* (B, GH, K, NY, UC). BAJA VERAPAZ: San Rafael Chilasco, Salama, *Guzmán V. 553* (F); Los Andes, Finca Panama, *Brenckle 47-201* (UC). IZABAL: Cerro San Gil, 300–900 m, *Steyermark 41908* (F). QUEZALTENANGO: Volcán Zunil, 1,500 m, *Skutch 976* (GH); Finca Pirineos, below Santa María de Jesús, 1,350–1,380 m, *Standley 68216* (F); road between Finca Pirineos and Patzulín, 1,200–1,400 m, *Standley 86710* (F); between Finca Pirineos and Patzulín, 1,200–1,400 m, *Standley 86744* (F, UC). SAN MARCOS: Barranco Eminencia, road between San Marcos and San Rafael Pie de la Cuesta, in upper part of the barranco between Finca La Lucha and Buena Vista, 2,500–2,700 m, *Standley 86332* (F). HONDURAS. COMAYAGUA: ca. 8 km SW of Siguatepeque, road to Jesús de Otoro, 1,200 m, *Burch 6114* (NY); near El Rincón, *Clewell 3097* (NY); Cerro Azul-Meambar, 1,100 m, *Horwath 72* (F), *74* (F). OLANCHO: 8.5 km W de Catacamas, márgenes del Río del Real, 900 m, *Ortega U. 295* (MO). PROV. UNKNOWN: Mr. Elliot's plantation, *Wilson 37* (NY). NICARAGUA. ZELAYA: Costado sur del Cerro La Pimienta, y N del Cerro

El Hormiguero, a orilla del Caño El Hormiguero, 800–900 m, 13°44′45″N, 84°59′45″W, *Grijalva 299* (UC); Costado SW de Cerro El Hormiguero, 900–1,000 m, 13°44′10″N, 84°59′50″W, *Grijalva 471* (UC); Cerro Saslaya, 1,100 m, *Neill 3820* (MO); Caño El Hormiguero, 750–800 m, 13°46′N, 84°59′W, *Pipoly 5929* (MO); trail toward Cerro El Inocente to Cerro Saslaya, 1,050–1,150 m, 13°46′N, 85°01′W, *Stevens 6677* (MO). COSTA RICA. ALAJUELA: near Cariblanco, along road to Colonia Virgen del Socorro, 800 m, *Burger et al. 11916* (F); forest along Río Sarapiquí upstream from crossing of road to Colonia Virgen del Socorro, 740 m, *Grayum & Hammel 5530* (CR, F, GH, MO); Reserva Forestal San Ramón, *Hernández 8608* (CR); Reserva Forestal de San Ramón, Río San Lorenzito, agua arriba a partir de la estación, 800–1,000 m, 10°12′53″N, 84°36′28″W, *Herrera Ch. et al. 339* (MO, UC), *Moran 4119* (CR, F, MO, UC), *Moran 4136* (CR, MO, UC); ca. 23 km NE of San Ramón, along Río La Balsa, 850 m, *Taylor 17819* (NY). CARTAGO: hills at N side of Río Navarro, between Río Sombrero and Quebrada Solon, W of El Muñeco, 1,260 1,400 m, 9°55′N, 83°48′W, *Grayum & Hammel 8466* (CR, MO, UC); E of Turrialba, road to Siquirres between Sabillas and Chitaría, ca. 1 km NE of Finca Mata de Caña, 900 m, *Lellinger & White 1431* (F, MO); 3 km SE of Cachí, 1,420 m, *Lent 2063* (CR, F); 22 km E of Turrialba, high ridge above Platanillo, 1,200–1,450 m, *Mickel 3401* (NY); 1 km E from Buenavista, 20 km NE of Turrialba, Río Chitaría, 750 m, *Saiki CR-59* (F); El Muñeco, 900 m, *Stork 2678* (UC). GUANACASTE: región del Volcán Cacao, Rancho Herold, 700–1,200 m, *Chacón & Chacón 2115* (CR). HEREDIA: OTS Field Station, banks of Quebrada El Saltito, 100 m, *Folsom 9735* (F, MO); Cacho Negro, Alto de los Quetzales, 1,700 m, *Gómez 2168* (F, GH, NY); Atlantic slope of Volcán Barva, along W fork of Río Sardinal, near future site of Rara Avis and to ca. 0.5 km upstream therefrom, 670–720 m, 10°17′N, 84°03′W, *Grayum 8506* (MO); Zona Protectora, between Río Peje and Río Guácimo, N slopes of Volcán Barba, 280 m, *Grayum & Schatz 3140* (CR); 9 km SW of Las Horquetas, between Quebrada Tigre and E fork of Río Sardinal, 600 m, *Grayum et al. 5060* (MO). LIMON: Hitoy Cerere reserve, SW of Valle La Estrella, ridge between Río Cerere and Quebrada Barrera, 150–550 m, 9°39′N, 83°02′W, *Grayum et al. 5808* (CR, MO, UC); Toro Amarillo, Guápiles, 350 m, *Lent 330* (GH); SE of Siquirres, Alto Guayacá, *Lent 1411* (F); Cantón de Talamanca, Croriña, Cerro Cruibeta, afluente de Quebrada Lumbeta, 9°25′15″N, 82°59′00″W, 550 m, *Herrera 3311* (MO, UC); SW of Guápiles, W side of Río Toro Amarillo, 1,000 m, *Rossbach 3860* (GH); Siquirres, 60 m, *Kupper 545* (M); Suerre, llanuras de Santa Clara, 300 m, *J. D. Smith 6885* (B, BM, F, G, GH, M, NY); Talamanca, forets de Tsâki, 200 m, *Tonduz 9473* (CR); 1901–1905, *Wercklé 1713* (NY, S). PUNTARENAS: Cordillera de Talamanca, area around Río Canasta, 9.5 km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier, 1,500–1,600 m, 9°02′N, 82°59′W, *Davidse et al. 28440* (AAU, CR, MO, UC), *28518* (UC); 5 km S of San Vito de Java, vic. of biological field station at Finca Wilson, 1,100–1,200 m, *Mickel 3143* (NY); Monteverde, 1,100 m, *Palmer 117* (NY). SAN JOSE: Tablazo, 1,900 m, *Brade 765* (B, M, NY, S, UC); Carillo, 400 m, *Kupper 528* (M); vic. of El General, 975 m, *Skutch 2715* (GH, MICH, MO, NY, S); 35 mi. S of Cartago, 5 mi. S of Santa María de Dota, 1,300 m, *Stork 1767* (GH, MICH, UC). PANAMA. CHIRIQUI: near Fortuna Dam, 1,200 m, *Hampshire & Whitefoord 212* (BM); ca. 3.5 km NW of Bajo Mono, along Río Caldera (Boquete region) and on slope to the east, 1,600 m, 8°50′N, 82°28′W, *Smith et al. 2455* (UC); no locality given, *Wagner 809* (M); Dtto. Boquete, Fortuna Dam site, Continental Divide, 1,100 m, *van der Werff & van Hardeveld 6766* (MO, UC). DARIEN: Serranía del Darién, Cerro Tacarcuna, 1,550–1,650 m, *Gentry 14069* (MO). PANAMA: Above Sta. Fé, beyond Escuela Agrícola, 1.8 mi. beyond fork in road on Pacific slope, *Croat 34167* (MO). VERAGUAS: Valley of Río Dos Bocas, road between Alto Piedra (above Sta. Fé) and Calovebora, 350–400 m, *Croat 27417* (MO). VENEZUELA. BARINAS: Dtto. Bolívar, entre Sto. Domingo y Altamira, en el sitio denominado Quebradón, en el camino que lleva al tunel que va hacia la represa, 1,300–1,500 m, *Ortega & van der Werff 2355* (MO, UC). MERIDA: Mérida, *Engel s.n.* (B). PORTUGUESA: Dtto. Sucre, Los Paramitos, 20 km por aire al SO de Biscucuy, 1,000–1,500 m, 9°20′N, 69°05′W, *Ortega et al. 1824* (MO, NY, UC); Dtto. Guanare, ESE of Paraíso de Chabasquén, along road to Córdoba, ca. 27 min. from Chabasquén, just below summit and below road, 1,500 m, 9°23′N, 69°54′W, *A. R. Smith et al. 1037* (MO, UC, Z). TRUJILLO: Dtto. Boconó, 33.5 km SE of Boconó, road to Guaramacál, 1,300 m, 9°12′N, 70°06′W, *A. R. Smith et al. 1545* (MO, UC). COLOMBIA. CUNDINAMARCA: Salto de Tequendamama, 2,300 m, *Cuatrecasas 194* (F). HUILA: Guadalupe, carretera vía a Florencia, a 2 km, 1,100 m, *Osorio 112* (COL). MAGDALENA: Santa Marta, above Onaca, 1,100 m, *H. H. Smith 968* (BM, F, GH, L, MICH, MO, S, UC). NARINO: Mpio. Ricuarte, along Río Imbí, 2–3 km above Ecopetrol Campamento Palmar, 3 km W of Ricuarte, 1,150 m, *Croat 71551* (MO); Ricuarte, entre Arrayán y Las Vegas, 1,400 m, *Mora 4087* (COL). SANTANDER: *Kalbreyer 857a* (B). TOLIMA: Casas de las Varones, *Stubel 16a* (B). ECUADOR. NAPO: Cascada San Rafael, km 101 via Lago Agrío, falls on Río Quijos, 1,275–1,375 m, *Foster 85-150* (UC); Archidona, Carretera Hollin–Loreto, Río Huatataraco, 800–1,000 m, *Cerón & Factos 7450* (MO, QCNE). PASTAZA: Colonia Játiva ca. 7 km N of Mera, 1,200–1,300 m, *Harling & Andersson 16908* (AAU, F, MO); 2 km al NE de Mera, Hacienda San Antonio del Barón von Humboldt, 1,300 m, *Baker et al. 5797* (MO).

*Asplenium riparium* grows on boulders along streams in wet forests from 200 to 1,900(–2,300) m. It ranges from Mexico to western Venezuela, Colombia, and Ecuador (Map 8).

The species is characterized by short-creeping rhizomes, petioles ⅓–½ the length of the lamina, and abaxially rounded (not carinate) rachises (Fig. 13A).

Since Liebmann's publication of *Asplenium riparium*, almost all pteridologists have considered it synonymous with *A. repandulum*. The two species clearly differ, however, by the rachidial characteristics used to separate them in the key. In addition, they differ in habitat: *A. riparium* grows on boulders along streams, while *A. repandulum* grows on tree trunks. The two species overlap in range only in eastern Ecuador (Maps 7, 8).

*Asplenium riparium* is most closely related to *A. volubile* because both have strongly carinate

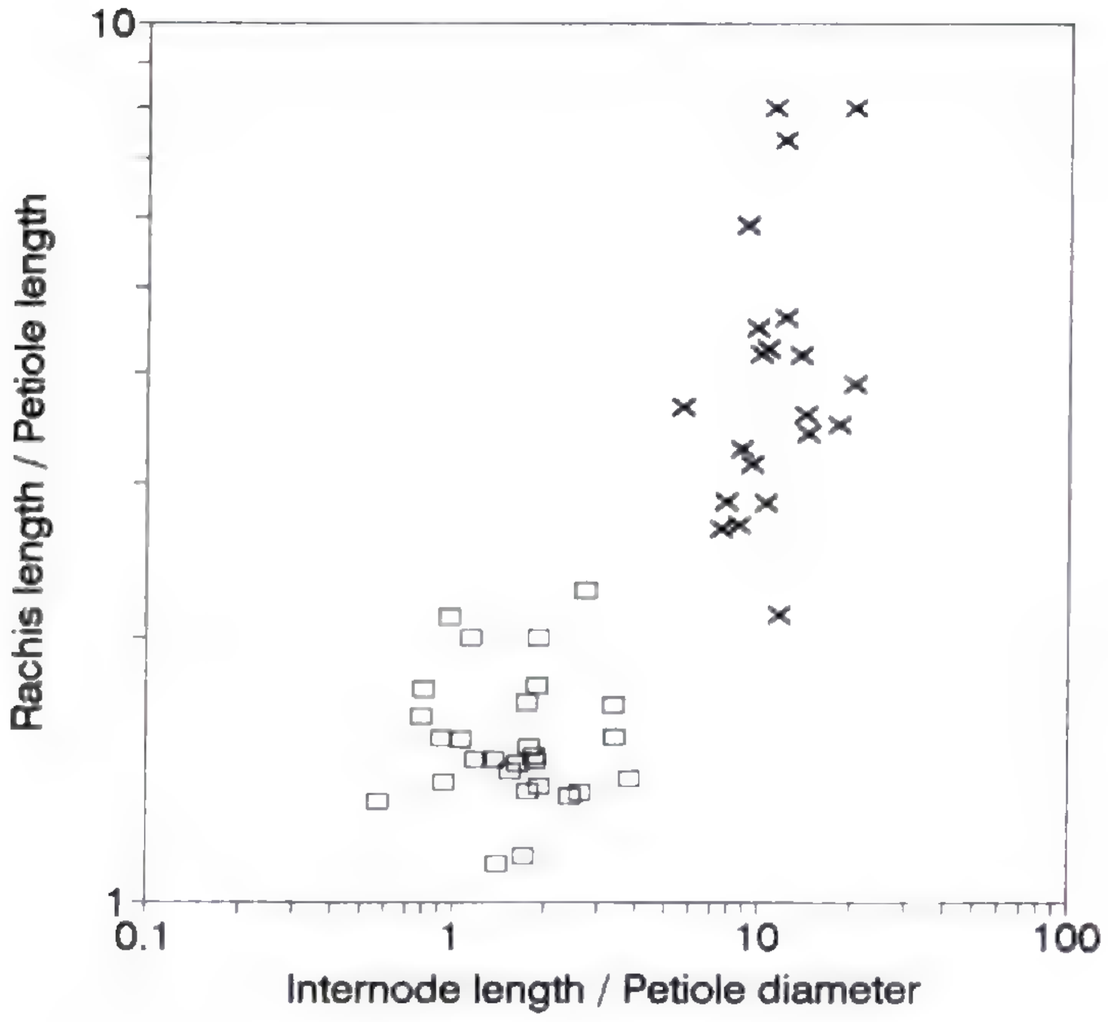



FIGURE 14. Quantitative differences between *A. riparium* (open squares) and *A. volubile* (X). The measurements were taken from herbarium specimens throughout the entire range of both species.

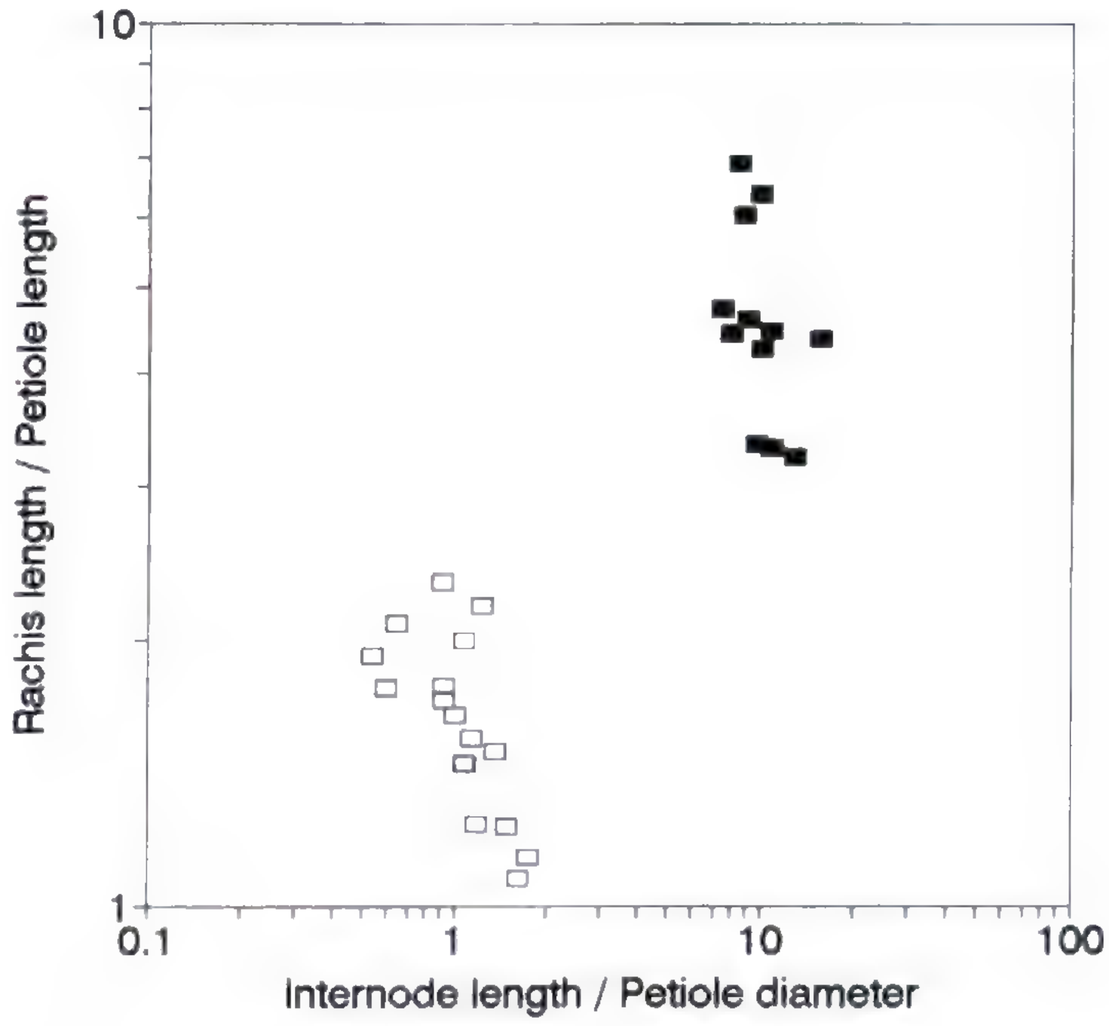



FIGURE 15. Variation in quantitative characteristics of *Asplenium riparium* (open squares) and *A. volubile* (black squares) from the Fortuna Dam area, Panama. The measurements were taken from living plants.

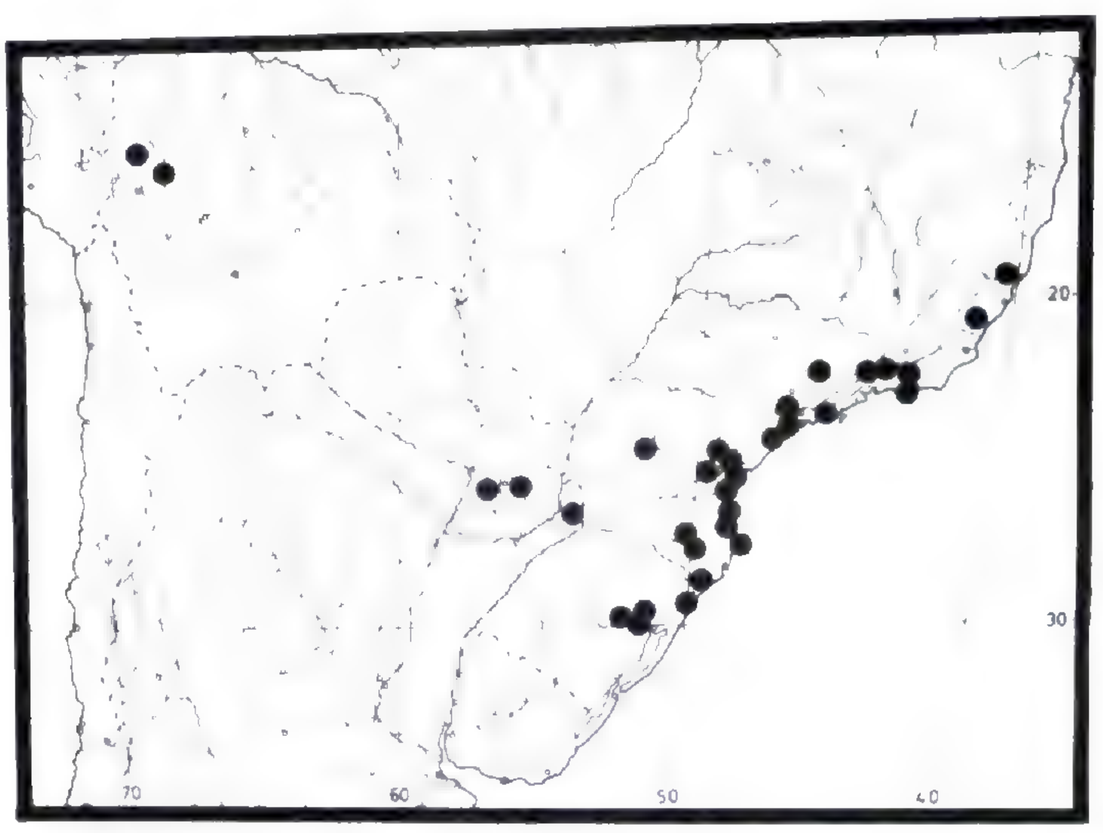
rachises. The two species are easily distinguished by the features given in the key. Petiole length relative to the lamina and internode distance clearly distinguish the two species (Fig. 14). Figure 15 shows that the two species maintain their distinctive characteristics even when growing in the same population.

The most remarkable thing about *A. riparium* is that it produces plantlets from the soral receptacles on senescent leaves that have drooped and touched the soil (Fig. 13C, D). Iwatsuki & Kato (1985) and Kato & Iwatsuki (1985) mentioned that several Old World species of section *Hymenasplenium* produce plantlets on the pinnae, but they did not specify whether the plantlets proliferated from the soral receptacles.

**9. Asplenium triquetrum** Murakami & R. C. Moran, sp. nov. TYPE: Bolivia. La Paz: Prov. Nor Yungas, Polo-Polo bei Coroico, 1,100 m, *Buchtien 625* (holotype, MO; isotypes, BM, K, NY, Z). Figure 8B, C; Map 9.

Plantae terrestres; rhizoma 2–6 mm latum, fere nudum, breviter reptans, internodis 0.4–2 cm longis; squamae 1–2.3 × 0.5–1.2 mm, ovatae, clathratae; laminae 22–40 cm longae, 1-pinnatae, 12–17 jugatae, lanceolatae vel oblongae, apice subconforme; rhachis triquetra, alis viridibus, ad laminam parallelis; pinnae 5 9 × 1.1 1.8 cm; venae 1–3 furcatae; sori 5–9 mm longi; sporae spinosae.

Plants terrestrial; roots 0.4–1.2 mm wide; rhizome 2–6 mm wide, nearly naked; scales 1–2.3 × 0.5–1.2 mm, dark brown, ovate, clathrate; petiole base 2–4 mm wide, swollen, 0.4–2 cm distant from each other on the same row; petiole 10–25 × 0.15–0.25 cm, ⅓–½ the leaf length, dark green-brown, fleshy and dull, glabrous, shallowly grooved; lamina 22–40 cm long, dark green, 1-pinnate, lanceolate to oblong with subconform apex; rachis with abaxial green wings in the same plane as the lamina, strongly carinate abaxially; lateral pinnae 5–9 × 1.1–1.8 cm in the middle of the leaf, 12–17 pairs, obliquely oblong to oblong-lanceolate, the margin occasionally lobed, almost entire to only slightly toothed, the basiscopic margin excavate for ⅐–⅓ the pinna length, acute at apex, broadly cuneate and almost sessile at base, auricle 2–6 mm long; veins 1–3 times forked; sori 5–9 mm long; spores 40–52 μm, 64 per sporangium, spiny.




MAP 9. The distribution of *Asplenium triquetrum*.

*Paratypes.* BOLIVIA. LA PAZ: Prov. Larecaja, Mapiri, 650 m, *Tate 401* (NY); 1,100 m, *Buchtien 3348* (GH, S). PARAGUAY. GUAIRA: Cordillera de Ybytyruzú, Cerro Peró, 1 km W of Destacamento Tororo, *Zardini 10966* (MO); Cerro Peró, 1 km W of Destacamento Tororo, around cave, 500 m, *Zardini & Aguayo 9501* (MO). PARAGUARI: Parque Nacional Ybycu'í, vecino al Salto Guaraní, *Aguayo 268* (MO). BRAZIL. PROV. UNKNOWN: *Glaziou 7247* (B); *Glaziou 7954* (B); *Glaziou 12283* (B); no locality, *Martius 342* (BM, L); São Pedro, Montenegro, 400 m, *Sehnem 2977* (B); Pinhal, Montenegro, 500 m, *Sehnem 6501* (B); Itajahy, *Ule 70* (B). ESPIRITO SANTO: Serra Tiutobá, Rio Docc., *Luetzelburg 7150b* (M, S). MINAS GERAIS: Caldas, *Mosen 2111* (GH). PARANA: Serra do Mar, inter Ypiranga ab Volta Grande, 600 m, *Dusén 3351* (MO, S); Ypiranga, *Dusén 3551* (S); Serra do Mar, Desvio Ypiranga, 700 m, *Dusén 6774* (G, S); Guaratuba, *Dusén 13730* (S); Serra do Mar, Desvio Ypiranga, 19 Sep. 1908, *Dusén s.n.* (BM, BR, F, G, GH, K, MO, NY, S, Z); Mpio. Morretes, Rio Mas Catira, 100 m, *Hatschbach 23237* (UC); Mpio. Morretes, Estr. Graciesa, Greta Funda, 500 m, *Hatschbach 24738* (MO, S, UC); Mpio. Morretes, Jurape, *Hatschbach 41961* (UC, Z). RIO DE JANEIRO: Organ Mts., 1837, *Gardener 168* (K); environs de Rio de Janeiro, *Glaziou 12289* (K); Sebastianipol, ad rivulos Mandioccae, *Martius s.n.* (B, K, M); Serra d'Estrella, Aug. 1817, *Martius s.n.* (M); Serra dos Orgãos, 1817, *Martius s.n.* (M); near Rio de Janeiro and Bahia, *Webb 66* (NY); Serra Estrella, *Luetzelburg 21* (M); Serra dos Orgãos, Morro Assu, Garganta, *Luetzelburg 6209* (M, S, UC), *Luetzelburg 6296a* (M); Serra Estrella bei Petropolis, wasserfall, 1,800 m, *Luetzelburg 6301* (M, MICH, UC); Serra Estrella, *Luetzelburg 6888* (F, K, M, MICH, UC); Serra Estrella bei Petropolis, *Luetzelburg 7396* (M); Corcovado, waterfall, 600 m, *Luetzelburg 13007* (M); Rio de Janeiro, *Mosén 2665* (B, K, S); Mandioca, *Sellow s.n.* (B). RIO GRANDE DO SUL: Sta. Cruz, Rio Cartichaninho, *Jürgens 372* (B, BM, M, S, UC); Sta. Cruz, Serra de Melo, *Jürgens 391* (S). SANTA CATARINA: Joinville, *Muller 186* (NY); Araranguá, *Reitz 729* (K, MO); Florianopolis, Sertão da Lagoa, *Rohr 1054* (B, L, NY); Pirabeiralea, *Schmalz 81* (S); Joinville, 800 m, *Schmalz 186* (F); Lages, *Spannagel 143* (NY, S, UC); Curitiba, *Viereck 1* (M). SAO PAULO: Iguape, 10 Sep. 1917, *Brade s.n.* (GH); Morro das Pedras, *Brade 5242* (S); Serra da Cantareira, prope São Paulo, 1,100 m, *Brade 6528* (GH); Cajuva, *Brade 8240* (GH, NY); Alto da Serra, *Edwall & Puttemans 5004* (S); *Luederwaldt 21480* (NY); Rio Grande, *Wacket 162a* (UC). ARGENTINA. MISIONES: Cordillera de Misiones, Picada a Carupimas de Américo, Salto del Encuentro, Río Piray, *Niederlein 1922* (B).

*Asplenium triquetrum* is the southernmost species of the section (Map 9). It grows from 400 to 1,100 m on wet rocks along deeply shaded streambanks, around cave entrances, and near small waterfalls.

*Asplenium triquetrum* is characterized by its epipetric habitat, strongly carinate rachis, and orientation of the rachidial wings in the same plane as the lamina (Fig. 8B, C). It is most closely related to *A. repandulum* (which see).

**10. Asplenium volubile** Murakami & R. C. Moran, sp. nov. TYPE: Ecuador. Cotopaxi: Quevedo–Latacunga road, km 46 from Quevedo, 600 m, 0°55′S, 79°11′W, *Holm-Nielsen et al. 2905* (holotype, MO; isotypes, AAU, F, UC). Figure 13E; Map 10.

Plantae epiphyticae; rhizoma 2.5–3.5 mm latum, fere nudum, longe reptans, internodiis 2–4 cm longis; squamae ovato-lanceolatae; laminae 22 35 cm longae, 1-pinnatae, oblongo-lanceolatae vel ovatae, apice conforme vel subconforme; rhachis abaxialiter rotundata, alis viridibus ad laminas perpendicularibus; pinnae 4–5.5 × 0.9–1.7 cm, 11 18 pares; venae 2-furcatae; sori 5–10 mm longi; sporae spinosae.

Plants epiphytic; roots 0.5–1.2 mm wide; rhizome 2.5–3.5 mm wide, nearly naked; scales 1–1.3 × 0.2–0.4 mm, brown, ovate-lanceolate; petiole base 2.2–3.8 mm wide, swollen, 2–4 cm distant from each other on the same row; petiole 4.5–11 × 0.1–0.25 cm, ⅐–¼ the leaf length, dark green-brown, fleshy and dull, shallowly grooved; lamina 22–35 cm long, dark green, 1-pinnate, oblong-lanceolate to ovate with a conform to subconform apex, thin-herbaceous; rachis like petiole, with green wings perpendicular to the plane of the lamina; lateral pinnae 4–5.5 × 0.9–1.7 cm in the middle of the leaf, 11–18 pairs, oblong-lanceolate, the margin only slightly toothed, excavate ⅛–⅓ portion of the basal basiscopic side absent, acute-obtuse at apex, broadly cuneate and almost sessile at base, auricle 1.5–5 mm long; veins 2-forked; sori 5–10 mm long; spores 48–50 μm, 64 per sporangium, spiny.

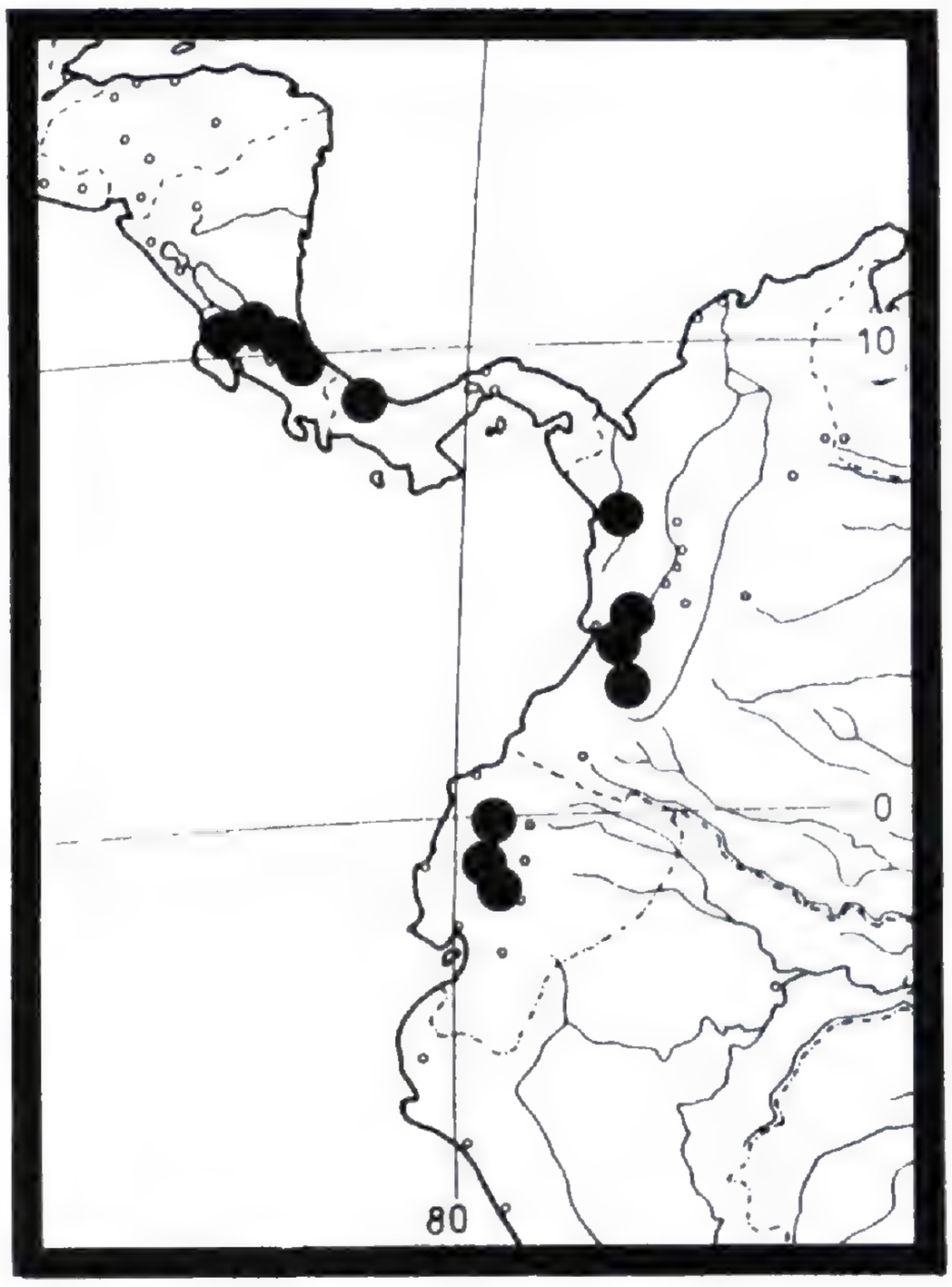
*Paratypes.* COSTA RICA. ALAJUELA: Upala, Bijagua, El Pilón, Río Celeste, 700 m, 10°49′N, 84°27′W, *Herrera 1248* (CR, F, MO, UC); SW of Cariblanco, between Río Cariblanco and Quebrada Quicuyal, canyon of Río Cariblanco and W slope and summit of ridge, 840 950 m, 10°16′N, 84°12′W, *A. R. Smith et al. 1875* (CR, MO, NY, UC). GUANACASTE: border with Alajuela, above Bijagua, slopes of Miravalles, 1,500 m, *Gómez et al. 19195* (MO, UC). LIMON: 5 km SW de Guápiles, bosque cerca del Río Toro Amarillo, 300–400 m, *Jiménez M. 2816* (CR, F, NY). PANAMA. BOCAS DEL TORO: along Continental Divide from road, branching N off main Fortuna–Chiriquí hwy. near Continental Divide, 1.1 mi. from main hwy., 1,200 m, 8°44′N, 82°17′W, *Croat & Grayum 60307* (MO, UC); 5.3 mi. N of bridge over Fortuna Dam, between Fortuna and Chiriquí Grande, 1.2 mi. N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat & Grayum 60425* (MO). COLOMBIA. CHOCO: San José del Palmar, hoya del Río Torito (afluente del Río Hábita), declive occidental, Finca "Los Guaduales," 630–730 m, *Forero et al. 6840* (COL, MO), *7237* (COL, MO). HUILA: Cordillera Oriental, vertiente occidental, abajo de Gabinete en la hondonada del Abra de San Andrés, 1,900–2,100 m, *Cuatrecasas 8607* (F). VALLE: arriba de La Glorieta, camino a Miralindo, Cordillera Occidental, vertiente oriental, Hoya del Río Cali, vertiente derecha, Quebradahonda, 2,100–2,250 m, *Cuatrecasas 18441* (COL, F, G); El Silencio, Yanaconas, 1,900–2,200 m, *Killip & García 33811* (COL, GH). ECUADOR. COTOPAXI: "Andes Quitensis," Chimborazo, *Spruce 5689* (G, K). LOS RIOS:

Cerro Mombe, Hacienda Clementina on Río Pita, 660 m, *Asplund 5550* (S); Hacienda Clementina, Samana, 750 m, *Harling 552* (S). NAPO: slopes of Guagra Urcu, on the loma above Río Bretania, 200–2,200 m, 0°28′S, 77°45′W, *Holm-Nielsen et al. 26835* (AAU). PICHINCHA: Toachi ad San Miguel, *Sodiro 66* (UC).

*Asplenium volubile* occurs in Costa Rica, Panama, and coastal Colombia and Ecuador (Map 10). It grows from 300 to 2,200 m in wet forests as an epiphyte on small trees or saplings.

*Asplenium volubile* has been previously identified as *A. repandulum*. In addition to the rachis characteristics given in the key, it differs from *A. repandulum* by its shorter petiole (4.5–11 cm long), which is only ⅐ to ¼ the leaf length (petiole 10–25 cm long and about ⅓ the leaf length in *A. repandulum*). In both species the rhizome is long-creeping and epiphytic, but field observations by both of us have shown that the rhizomes differ in habit. *Asplenium volubile* has a twining rhizome that grows spirally around the trunks of young trees or saplings that are usually less than 5 cm wide. This characteristic can usually be ascertained in herbarium specimens because the rhizomes appear sinuous or contorted. In contrast, *A. repandulum* grows on large trees and the rhizome is more or less straight, not spiraling upward around the trunk. *Asplenium volubile* has a longer-creeping rhizome than *A. repandulum*. The distance between petiole bases on the same side of the rhizome (orthostichy) is 2.2–3.8 cm in *A. volubile*, and 0.4–2 cm in *A. repandulum*. In addition to the morphological characteristics, the two species differ completely in range: *A. volubile* is restricted to the western side of the Andes (Map 10) and *A. repandulum* is restricted to the eastern side (Map 7).

See *A. riparium* for comparison to that species.




MAP 10. The distribution of *Asplenium volubile*.

HYBRIDS

**11. Asplenium ×papyraceum** (Jermy & T. Walker) Murakami & R. C. Moran, comb. nov. *Diplazium ×papyraceum* Jermy & T. Walker, Bull. Brit. Mus. (Nat. Hist.), Bot. 13: 264, fig. 10. 1985. TYPE: Trinidad. Charuma Ward: Central Range Forest Reserve, Brickfields Teak Plantation, 3 mi. S of Forest Resthouse, 60 m, in wet ground by stream, 9 July 1963, *Walker T6178* (holotype, BM not seen).

Plants terrestrial; rhizome 2–3 mm wide, sparsely scaly; scales 1–1.5 mm long, narrowly lanceolate, blackish, entire; petiole base 2–3 mm wide, ca. 1 mm distant on the same row; petiole 15–22 cm long, brown, slightly shorter than the lamina, gray-green with narrow black wings, glabrous; lamina 25–30 × 12–17 cm, 1-pinnate, ovate-lanceolate, the apex abruptly to gradually reduced, pinnatifid; rachis brown, sparsely scaly with minute (0.5–1 mm long) filiform, unicostate scales and slightly longer, narrowly triangular scales; pinnae 7–8.5 × 1.5–2.2 cm, short-petiolulate, 9–12 pairs, the basal basiscopic margin slightly excavate, the acroscopic margin coarsely serrate, the serrations 1–2 mm deep; veins 2 or 3 times forked; sori 3–11 mm long; spores abortive.

*Specimen examined.* TRINIDAD. CHARUMA WARD: Central Range Forest Reserve, Brickfields Teak Plantation, 3 mi. S of Forest Resthouse, 60 m, in wet ground by stream, 9 July 1963, *Jermy 2178* (BM).

*Asplenium ×papyraceum* is known only from the above-cited locality in Trinidad. Jermy & Walker (1985) have an excellent photograph of the paratype (*Jermy 2178*). The plants resemble *A. delitescens* but differ by their shorter, relatively wider, and more numerous pinnae.

*Asplenium ×papyraceum* is believed to be a hybrid based on its irregular meiosis, two size classes of chromosomes, triploid chromosome number, and abortive spores (Jermy & Walker, 1985). The asplenioid characteristics of *A. ×papyraceum* are clathrate scales and an X-shaped petiolar strand that unites distally in the petiole. It belongs to section *Hymenasplenium* as evidenced by its short-creeping rhizome with a typical broad ventral meristele and by its rachis-costa structure.

Jermy & Walker (1985) discussed the evidence relating the hybrid to *Asplenium*, but concluded that it belonged in *Diplazium* based on the chromosome count of $n = 123$, a multiple of 41, which is the base number for *Diplazium*. The count of $n = 123$, however, does not exclude *Asplenium*. Although a base number of 41 is not known in *Asplenium*, it is not far off from the numbers known in section *Hymenasplenium*, which have $n = 38$ or 39 (Mitui et al., 1989). The most likely explanation of $n = 123$, given the morphological evidence that clearly indicates the plant is an *Asplenium*, is that the parents had the unusually high chromosome number of $n = 41$. The resemblance to *A. delitescens* suggests that that species is one of its parents; however, *A. delitescens* is not known from Trinidad (Map 2).

**12. Asplenium delitescens** (Maxon) L. D. Gómez × **A. laetum** Sw. Figure 6B.

The specimens listed below are presumably hybrids based on their intermediate morphology between *A. delitescens* and *A. laetum*.

*Specimens examined.* BELIZE. STANN CREEK: Stann Creek Railway, 50 m, *Schipp 49* (BM, MICH, MO, UC). COSTA RICA. ALAJUELA: Río Chiquito, ca. 40 km on road to Upala, 800 m, *Gómez 18620* (MO, UC). SAN JOSE: Zona Protectora El Rodeo, along Fila Diamante, S from Alto Gracias a Dios, 4 km (by air) SW of Ciudad Colón, 900 m, *Grayum & Zamora 9661* (MO, UC). VENEZUELA. ARAGUA: near Guamitas, Parque Nacional, 760 m, *Alston 5828* (MO). FALCON: Parque Nacional Quebrada de la Cueva El Toro, steep, wet valley along river, 600 m, *Liesner et al. 7724* (MO, NY, UC). COLOMBIA. BOLIVAR: Mpio. de San Jacinto, ca. 16 km NW of San Jacinto, N slope of Cerro Maco, 600 m, *Zarucchi & Cuadros 4040* (MO). MAGDALENA: 7 km E of Codazzi, 300 m, *Haught 3761* (COL, GH). META: La Macarena, Río Gúejar ca. 10 km below junction with Río Zanza, 470 m, *S. G. Smith & Idrobo 1523* (COL, GH, UC). ECUADOR. MORONA-SANTIAGO: Cordillera de Cutucú, road Méndez–Morona, 800 m, *van der Werff & Palacios 10403* (F, MO, QCNE). NAPO: Parque Nacional Yasiní, Anangu, Río Anangu near junction with Río Napo, 270 m, *Luteyn et al. 8502* (NY, UC). PERU. HUANUCO: ca. pueblo de Puerto Inca, a unos 85 km de la confluencia con el Río Ucayali, 400–500 m, *Schunke V. 2967* (NY). LORETO: above Pongo de Manseriche, 250 m, *Mexia 6223* (BM). MADRE DE DIOS. Manú, Parque Nacional Manú, Pakitsa Station, Tachigali Trail to 8 km N of camp, 350 m, 11°56′S, 71°16′W, *Foster & Baldeón 12806* (F). BOLIVIA. BENI: Prov. Ballivián, Río Colorado, Collegio Técnico Agropecuario de Río Colorado, 235 m, 15°00′S, 67°10′W, *Fay 2078* (MO). LA PAZ. Prov. Larecaja, Isupuri, 500 m, *Williams 1091* (GH, NY); Prov. Nor Yungas, puente sobre el Río Beni, 550 m, *Beck 13367* (F).

The above specimens would key to *A. laetum* because of their number of pinna pairs (10–21) and atropurpureous petioles and rachises. These intermediates differ from *A. laetum* by their larger laminae and often abruptly contracted apices. The above specimens differ from *A. delitescens* in the shape of the lamina apices (especially the shape of the pinnae below the apical segment), greater number of pinna pairs, and dark petioles (Fig. 6B). The shape of the lamina apex is perhaps the best characteristic to detect the intermediates, but it is difficult to characterize the plants because of their inherent variability in features that distinguish the parents.

Most of the specimens have aborted spores, but some appear to have normal spores. The specimens treated here need to be investigated cytologically and enzymatically to confirm their hybridity and determine their parentage. A few may eventually be shown to have *A. ortegae* or *A. purpurascens* as the other parent.

**13. Asplenium ×incisoserratum** (Rosenstock) Murakami & R. C. Moran, stat. nov. *Asplenium laetum* Sw. var. *incisoserratum* Rosenstock, Repert. Spec. Nov. Regni Veg. 22: 8. 1925. TYPE: Costa Rica. San José: Grenadilla, 1,200 m, 26 Dec. 1910, *Brade 425* (holotype, S; isotypes, B, M, UC). Figure 16.

Plants epilithic; roots 0.1–0.5 mm wide; rhizome 2–4 mm wide, scaly at the apex; scales 2–2.5 × 0.25–0.35 mm, blackish, narrowly triangular to linear; petiole base 0.5–2 mm wide, swollen, 1–1.5 mm distant from each other on the same row; petiole 3–8 × 0.03–0.1 cm, ca. ⅛–⅓ the leaf length, mostly stramineous to greenish, sometimes brown basally (especially in large leaves), glabrous; lamina 8–20 cm long, green, 1-pinnate, lanceolate, gradually to abruptly tapered to a pinnatifid apex; rachis greenish; lateral pinnae 1.4 × 0.5–1 cm, 6–14 pairs, lanceolate, acute to obtuse, coarsely dentate, the teeth 1–2 mm deep, the basal basiscopic side excavate for ⅓–½ the length of the pinna; veins 1-forked; sori 3–5 mm long; spores irregular, aborted.

*Additional specimens examined.* MEXICO. OAXACA: Tuxtepec, above Jalapa de Díaz, 330 m, *Hallberg 1467* (NY). COSTA RICA. CARTAGO: Río Reventazón, below Turrialba, 540–600 m, *Skutch 4681* (CR, F, GH, MO). SAN JOSE: Río Surubres, 300 m, *Brade 430* (B, GH, M, S, UC); vic. of El General, 1,100 m, *Skutch 2531* (MICH, MO, S); basin of El General, 675–900 m, *Skutch 4790* (CR, MICH, MO). TRINIDAD. No locality, *Fendler 61 pro parte* (B, GH, MO). COLOMBIA. VALLE: valley of Río Digua, 950 m, *Alston 7837* (MO).

*Asplenium ×incisoserratum* grows on wet cliffs and boulders in streams from 300 to 1,200 m.

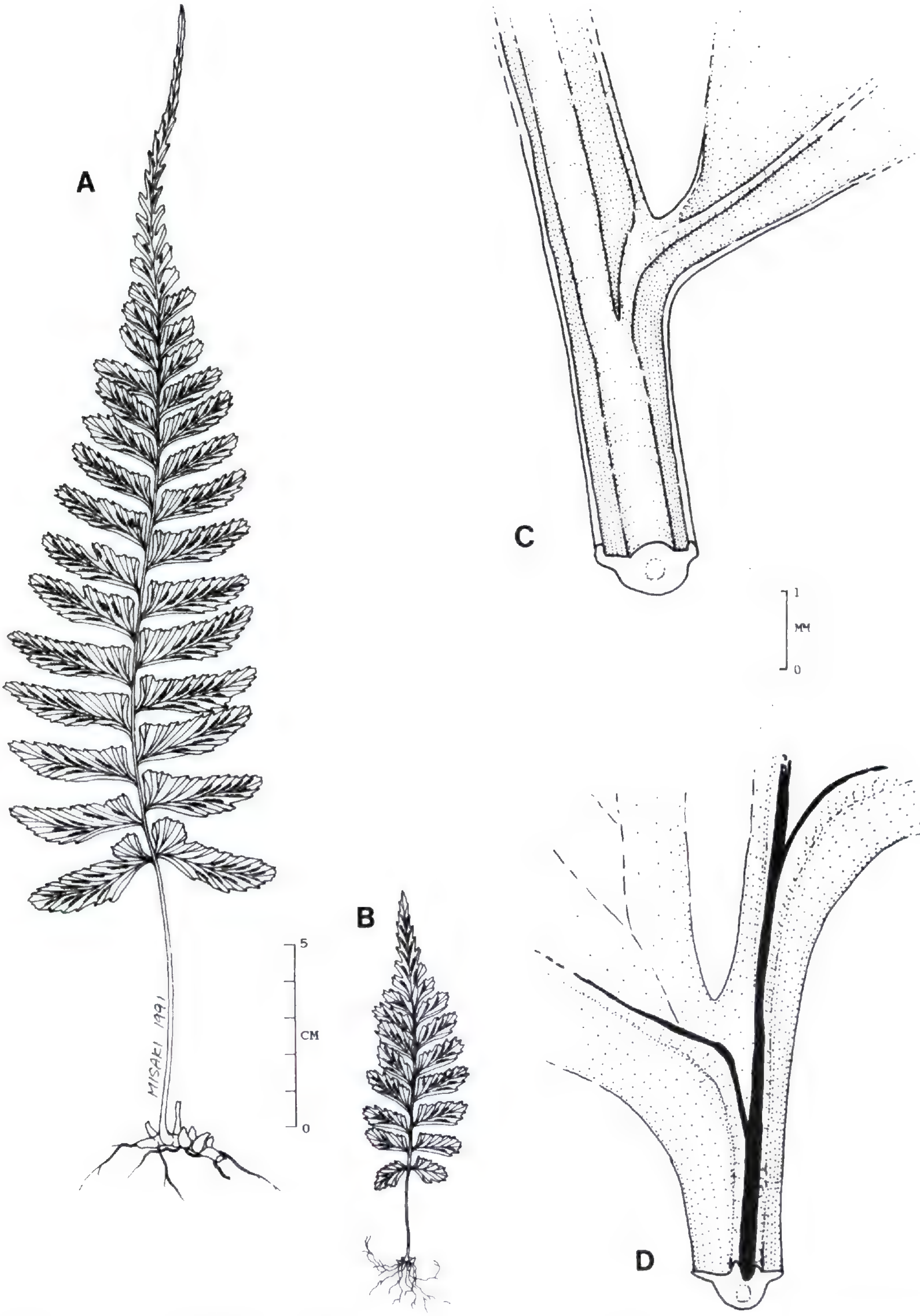



FIGURE 16. A, B. *Asplenium* ×*incisoserratum* (*Brade 430*, GH).—A. Large fertile leaf.—B. Small fertile leaf.—C. *A. abscissum*, juncture of rachis and pinna, note the raised, ungrooved rachis and costa, and thickened decurrent pinna margins (*Skutch 2339*, MO).—D. *A. delitescens*, juncture of rachis and pinnae, note the grooved rachis and the narrow wing that borders the costules and the rachidial groove (*Martínez S. 16399*, MO).

Based on morphology (Fig. 16), it appears to be a hybrid between *A. hoffmannii* and *A. laetum*. From *A. hoffmannii*, it differs by having more pinna pairs, more than two or three leaves per rhizome, and a basally darkened petiole (especially in large leaves). From *A. laetum*, it differs by its usually greenish petiole, greenish rachis, fewer number of pinna pairs, and more deeply and thoroughly incised-serrate pinnae. All of the specimens cited above have aborted spores.

Two miscellaneous notes: The specimen cited from Colombia appears to be this hybrid, but *A. hoffmannii* is not known from western Colombia where the specimen was collected. Apparently, Rosenstock (1925) did not publish a new name when referring to *Brade 430* as representing a "forma minor, die vorliegenden Exemplare fruktifizieren schon bei 6 cm Höhe." This diagnosis is in German, contrary to Rosenstock's varieties in the same paper, which are in Latin. Also, the typography of "forma minor" is in roman, not boldface or italic as he usually used when publishing new names.

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## Index to Collectors' Names and Numbers

This monograph is based on the specimens cited below, which consist of about 1,800 herbarium sheets representing approximately 780 gatherings from 22 herbaria (see acknowledgments for list of herbaria). Types are in boldface. The numbers in parentheses refer to the number of the species and hybrids in this monograph, given below for easy reference.

### SPECIES

1. A. delitescens (Maxon) L. D. Gómez
2. A. hoffmannii Hieron.
3. A. laetum Sw.
4. A. obtusifolium L.
5. A. ortegae Murakami & R. C. Moran
6. A. purpurascens Mett. ex Kuhn

7. A. repandulum Kunze
8. A. riparium Liebm.
9. A. triquetrum Murakami & R. C. Moran
10. A. volubile Murakami & R. C. Moran

HYBRIDS

11. A. ×papyraceum (Jermy & T. Walker) Murakami & R. C. Moran
12. A. delitescens × A. laetum
13. A. ×incisoserratum (Rosenstock) Murakami & R. C. Moran

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L'Herminier 18 (3); 79 (4); 169 (4). Lehmann 8830 (5). Lellinger 517 (3); 571 (4). Lellinger & White 1431 (8). Lellinger & de la Sota 532 (1); 550 (3). Lent 330 (8); 1411 (7); 2063 (8); 4061 (3). Leonard & Leonard 14363 (3). Liebmann **310** (8); **322** (3). Liesner & González 9473 (1). Liesner et al. 7724 (12). Linden 31 (8); 68 (8). Lindig 236 (3). Little & Little 8427 (5). Lloyd 698 (4); 699 (3); 871 (4). Lojtnant 15757 (3). Losch 770 (3). Luederwaldt 21480 (9). Luetzelburg 21 (9); 6209 (9); 6296a (9); 6301 (9); 6888 (9); 7150b (9); 7396 (9); 13007 (9). Luteyn et al. 8502 (12).

Maas et al. P12902 (5). Madriñán & Barbosa 258 (4). Martínez 9 (1). Martínez S. 8008 (1); 8136 (1); 8402 (1); 16399 (1). Martínez S. et al. 22711 (3). Martius

342 (9). Matuda 221 (8). Maxon 623 (3); 641 (3); 2545 (3); 4158 (3); 4677 (1); 4868 (3); 5055 (3); 5733 (3); 9057 (3). Maxon & Harvey 6674 (1). Maxon & Hay 3263 (8). Maxon & Killip 244 (3); 772 (3). Maxon et al. 6807 (1). McDonagh et al. 446 (3). McPherson 8666 (4). Mendonca 1208 (3). Mexia 6223 (12). Mickel 1087 (8); 1304 (2); 1434 (8); 1862 (3); 2061 (3); 2317 (3); 3143 (8); 3359 (3); 3401 (8); 5650 (8); 5784 (1); 5881 (3); 5893 (8); 5918 (8); 6077 (2); 6360 (8); 6446 (8); 6461 (3); 6715 (8); 7172 (8); 7188 (3); 7212 (1); 7411 (2); 9446 (4); 9516 (3). Mickel & Leonard 5138 (2); 5177 (2). Mickel & Pardue 6548 (8); 6580 (8); 6843 (1); 6866 (1). Moore 7 (3). Mora 4087 (8). Morales R. 65 (1). Moran 3092 (3); 3121 (3); 3676 (1); 3683 (3); 4119 (8); 4136 (8); 5329 (6). Moreno 19063 (1). Mori & Kallunki 2670 (2); 2672 (1); 2826 (3); 3964 (4). Moritz 23 (3); 365 (3); 384 (4). Morton 6170 (4). Morton & Makrinius 238 (3). Mosén 2111 (9); 2665 (9); 3736 (3). Müller 186 (9); 1772 (8); 1835 (3). Murillo 363 (3); 2197 (5). Murray 26 (3).

Nash 199 (3). Nee 7722 (3); 9026 (1); 9456 (3); 29974 (1). Nee & Schatz 19943 (8). Neill 3820 (8). Niederlein 1922 (9).

Ocampo S. 1637 (3). Øllgaard et al. 39205 (3). Orcutt 6835 (3). Ortega 1912 (5). Ortega & Aymard 1817 (5); 1818 (3); 2087 (5); 2088 (5); 2089 (2). Ortega & González 365 (4). Ortega & R. F. Smith 2440 (4). Ortega & Stergios 1467 (3). Ortega & van der Werff 2358 (4); 2348 (4); 2355 (8). Ortega U. 295 (8). Ortega et al. 1824 (8); 1845 (3); 1886 (3); 3093 (6). Osorio 112 (8). Otto 176 (3); 609 (3).

Palmer 117 (8). Pannier 132 (4). Pavón 186 (3). Pennell 4213 (1). Pérez 1 (6). Pipoly 4861 (3); 5929 (8). Plowman & Schunke V. 7363 (7). Polakowsky 151 (3). Pollard & Palmer **348** (1). Prestoe 714 (3). Pringle 7889 (8). Proctor 4069 (3); 17250 (3); 17254 (4); 17703 (4); 19252 (3); 21691 (4); 22690 (3); 36071 (3). Proctor et al. 27114 (1). Purpus 174 (3); 1983 (8); 2846 (8); 2946 (8); 6735 (3); 6765 (3); 7241 (3); 15420 (8).

Quijada 103 (3).

Reitz 729 (9). Riba et al. 318 (8). Rivera 23 (1). Rohr 1054 (9). Ross 688 (3). Rossbach 3860 (8). Rovirosa 828 (3); 1038 (1); 3135 (1). Rowlee & Rowlee 415 (1).

Saiki CR-59 (8); M234 (1); M230 (3). Sandwith 1790 (4); 1833 (3). Schipp 8-275 (1); 49 (12); S-277 (3). Schlim 397 (3); 653 (4). Schmalz 81 (9); 186 (9). Schott 51 (3); 57 (1); 755 (3). Schunke 20 (3); 4909 (3). C. Schunke 155 (7); 897 (7); 907 (7). Schunke V. 2967 (12); 2967 (1); 3261 (3). Seaverns 13 (3). Seemann 66 (1); 72 (2); 369 (2). Sehnem 2977 (9); 6501 (9). Seibert 583 (1); 587 (1). Seifert 42 (3). Seiler 718 (2). Seymour 6200 (2). Shattuck 189 (1); 283 (3). Sherring 87 (3); 131 (4). Shillingford & Adams 98 (4). Sieber 363 (4). Sintenis 6271 (4); 6443 (4); 6533 (4). Skutch 976 (8); 2531 (3); 2715 (8); 4681 (13); 4790 (3). Smith 358 (3); 1121 (3); 1362 (3); 2449 (3); 5168 (7); 5675 (1). Smith et al. 1340 (1); 1710 (3); 2455 (8); 1620 (3). A. R. Smith et al. 856 (2); 1037 (8); 1062 (5); 1095 (2); 1545 (8); 1620 (3); 1875 (10); 1961 (2); 2455 (8). H. H. Smith 958 (3); 968 (8); 1126 (4); 2693 (1). H. H. Smith & G. W. Smith 710 (4); 961 (3); 2450 (3). J. D. Smith 6885 (8). S. G. Smith & Idrobo 1523 (12); 1523 (1). Sodiro 66 (10); 8.74 (6); 8.75 (6). Spannagel 143 (9). Sparre 17173 (6). Sperling 4945 (8); 4995 (8). Sperling et al. 6035 (1); 6381 (1). Spruce 5689 (10); **5697** (6). Standley 8744 (3); 11234 (3); 26184 (1); 27218 (2); 29372 (2); 52815 (3); 53554 (3); 54153 (1); 60656 (2); 68216 (8); 71321 (8); 86332 (8); 86710 (8); 86744 (8); 88974 (3); 89091 (3); 90658 (8); 90667 (8). Stern et al. 235 (1); 705 (3); 824 (1). Stevens 6677 (8). Stevens et al. 6582 (3). Steyermark 41908 (8); 44752 (3); 44894 (3); 45308 (1); 45507 (3); 49389 (3); 54407 (3); 61143 (3); 61148 (4); 61569 (4); 94822 (4); 99872 (3). Steyermark & Davidse 116306 (3); 116896 (4). Steyermark & Espinoza 112683 (4). Steyermark & Rabe 96232 (4). Steyermark & Steyermark 95249 (4). Steyermark et al. 121451 (4); 121514 (3); 121590 (4); 127064 (2); 127131 (5); 127134 (5); 127236 (2). Stork 1764 (3); 1767 (8); 2678 (8). Strudwick et al. 3574 (3). Stübel 16a (8); 878 (7); 1099a (7). Sytsma 2314 (2).

Tate 401 (9). Taylor 17819 (8). Thieme 4 (1); 5675 (1). Tonduz 9473 (8). Tryon 7399 (4). Tryon & Tryon 5228 (3). Tyson 2237 (2). Tyson et al. 4835 (1).

Ule 70 (9). Underwood 2304 (3); 2802 (3). Underwood & Earle 615 (3); 989 (3).

Valverde 510 (6). van der Werff 402 (1); 660 (7); 3403 (3). van der Werff & González **4599** (5). van der Werff & Palacios 10403 (12). van der Werff & van Hardeveld 6766 (8). van der Werff & TR 702 (4). Vásquez 977 (1); 2485 (1). Ventura A. 3267 (8); 14368 (8); 16002 (8). Viereck 1 (9). von Türckheim 630 (8); 2824 (3); 8048 (3).

Wacket 162a (9). Wagner 809 (8). Walden 41 (7); 84 (3). Walker **T6178** (11). Webb 66 (9). Welch 19856 (2). Wercklé 1713 (8); 17432 (1). Wetmore & Woodworth 105 (1). Whitefoord 4174 (4); 4549 (4); 6164 (3). Wiggins 11095 (6). Wilbur et al. 7473 (4). Williams 1026 (1); 1076 (3); 1076a (3); 1091 (12). Wilson 37 (8); 161 (3); 280 (3); 577 (3). Witherspoon & Witherspoon 8797 (1). Woodson et al. 1601 (2). Wright 1026 (3); 1027 (3); 1086 (3).

Zardini 10966 (9). Zardini & Aguayo 9501 (9). Zuluaga R. 986 (1); 332 (3).

# A REVISION OF THE GENUS *PLEUROTHYRIUM* (LAURACEAE)[1]

*Henk van der Werff*[2]


## Abstract

*Pleurothyrium*, a genus of Lauraceae mostly consisting of trees, ranges from Guatemala to Bolivia and possibly Southern Brazil. The genus is best represented in Peru, Ecuador, and Colombia and mostly occurs at low elevations. In this revision 39 species are included in *Pleurothyrium*, of which 19 are described as new. Taxonomic history, characters, and phylogenetic classification are discussed. Data on phenology, habitat preference, and altitudinal range are presented when available.


In the course of identifying neotropical Lauraceae accumulated in MO or received on loan from other institutions, I found several undescribed species of *Pleurothyrium*. Four of those were published in earlier papers (van der Werff, 1987, 1988), but because the number of novelties kept increasing, I decided that writing a revision of the genus was the best way to deal with the many new species. Notable among those are the collections by J. Cuatrecasas from Chocó and Valle, Colombia, which include three striking, undescribed species. Recent collections by Missouri Botanical Garden staff members have also added significantly to the number of species. In this paper 19 species of *Pleurothyrium* are described, which brings the number of accepted species to 39. Because so many undescribed species were collected recently, I anticipate that the number of *Pleurothyrium* species will continue to grow. Another indication of this future growth is that 12 species are known from the type collection only, and an additional seven are known from two collections. Only three species have been collected more than 20 times. The large number of undescribed species found during this study shows clearly that our knowledge of neotropical Lauraceae is still incomplete. It is not coincidence that the largest percentage of undescribed species comes from Ecuador, a country where an active tree collecting program has been in place during the past seven years. Seven of the 12 *Pleurothyrium* species known from Ecuador are new to science.

There is little information available about economic uses of *Pleurothyrium* species. In central Peru the wood is used as timber and is considered to be of reasonably good quality. The wood of several Colombian species is used for making boards or canoes. It is likely that the wood of other species is also used locally, but because most of these species are rare and several do not grow into tall trees, their use is economically not very important.

## Materials

This revision is based on about 300 collections, some with many duplicates, found in many herbaria. A general difficulty with a generic revision in the Lauraceae is that many specimens are not identified to genus and therefore will not be sent when a loan of material of a particular genus is requested. One can solve this problem by personally selecting loans or by having a knowledgeable friend do so. In this case, Jens Rohwer kindly annotated all *Pleurothyrium* specimens in F, NY, and US to genus for me. In addition to these collections, I received loans from B, BM, BR, C, E, INPA, K, L, LE, P, S, U, UC, and VEN. I also had the opportunity to study the specimens of COL, IAN, MG, RB, and SP and thank the curators of these herbaria for loans and assistance during my visits. Recent collections by Missouri Botanical Garden botanists (notably B. Hammel, Costa Rica and Panama; G. McPherson, Panama and Colombia; A. Gentry, Colombia and Peru; C. Dodson, Ecuador;

[1] This study would not have been possible without the collecting efforts of many collectors, especially J. Cuatrecasas and Missouri Botanical Garden staff members, as well as the often large loans I received from several herbaria. I gratefully acknowledge their contributions. J. Crisci's assistance with the cladistic analysis is gratefully acknowledged. I thank several botanists (C. Berg, G. McPherson, R. Moran) who tried out the key and suggested improvements. The illustrations, both older and new ones, were made by J. Myers. The project was supported by National Science Foundation grant BSR-8918096.

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D. Neill, Ecuador; C. Cerón, Ecuador; W. Palacios, Ecuador; R. Vásquez and J. Jaramillo, Peru) have contributed a great deal to this study.

## Taxonomic History and Generic Relationships

The genus *Pleurothyrium* was published by Nees in Lindley's *Natural System of Botany*, ed. 2, which appeared in July 1836 fide *Taxonomic Literature 2*, followed soon (October 1836) by a more detailed treatment in Nees's *Systema Laurinarum*. Initially, Nees included two species, *P. chrysophyllum* and *P. bifidum*, in his genus but added in his *Systema Laurinarum P. poeppigii* and *P. cuneifolium*. He described the genus as having six staminal glands and characterized it by the large glands and the lateral anther cells, which open back-to-back. Nees did not designate a type species. Bentham & Hooker (1880) expressed the opinion that *P. chrysophyllum* Nees fits the generic description best, and this species has been generally accepted as the lectotype species (Pax, 1889; Kostermans, 1952; Rohwer, 1986). In 1848, Nees described a fifth species of *Pleurothyrium*. Meissner (1864) added three species to *Pleurothyrium*, all of which are now placed in other genera. In his generic description, he mentioned the presence of a hypogynous disk forming a narrow ring on which stamens and glands are inserted. Meissner also stated that only six glands were present at the base of stamens of whorl III and that the staminodia do not possess glands at their base, this in contrast to Nees (1836a, b), who reported glands at the base of the staminodia. Baillon (1870) essentially accepted Meissner's circumscription of the genus; he stated that the disk was situated in the receptacle and that its apex was curved inward. The number of staminal glands remained six. Bentham & Hooker (1880) described *Pleurothyrium* as having a fleshy disk with six lobes alternating with six stamens, this in contrast to earlier authors, who described the disk as a narrow ring. Bentham & Hooker (1880) also mentioned the presence of glands at the base of the stamens of whorl III but did not describe how the glands are placed in relation to the disk. Actually, their description of the disk applies to the glands; the later confusion between disk and glands has its beginning here. Pax's description (1889) is brief and essentially the same as Bentham & Hooker's. Mez (1889) did not mention the presence of a disk in his description of *Pleurothyrium* but stated that all nine stamens had two glands at their base, which were almost always fused. In comparison to Nees's description, two other differences are noteworthy: Mez did not mention staminodia in his generic description, but Nees included biglandular staminodia in his description; according to Mez, the outer six anthers have two introrse and two extrorse, rarely lateral dehiscing locelli, whereas Nees described the locelli as lateral. Mez was the last person to revise *Pleurothyrium*; he excluded the three species Meissner (1864) described, but added one species described by Meissner (1864) as a *Nectandra*. Mez recognized five species in the genus. In the 1930s, several species of *Pleurothyrium* were described (Ducke, 1930; Smith, 1935; Schmidt, 1928, 1933) without any change in generic circumscription. MacBride (1938) essentially accepted Mez's description of the genus. Lasser (1942) described two Venezuelan species of *Pleurothyrium*, but did not discuss the generic concept. Kostermans (1952, 1957) looked critically at the validity of *Pleurothyrium* as a genus. He found that *Pleurothyrium* only differed from *Ocotea* in the position of the anther cells and the presence of glands at the base of all stamens. In his opinion, these differences were not sufficient for the recognition of *Pleurothyrium* as a genus, and he proposed to treat it as a section (1952) or subgenus (1957) of *Ocotea*. In 1952, he formally transferred all *Pleurothyrium* species to *Ocotea*. Bernardi (1962) followed Kostermans and treated *Pleurothyrium* as a subgenus of *Ocotea*. His description, however, partly followed Meissner: he mentioned a disk in the form of a narrow ring with the stamens inserted on the ring, but differed from Meissner in crediting all stamens with glands at their bases. Hutchinson (1964) fell back on Bentham & Hooker's concept of *Pleurothyrium*, with fleshy disk, this with six teeth alternating with the stamens as well as glands at the base of the inner three stamens. He accepted five species, half the number Kostermans (1952) included. Allen (1966b) discussed the concept of *Pleurothyrium* in detail and concluded that it deserved generic status, characterized by the presence of glands at the base of all stamens and the position of the anther cells. It is worth noting that Kostermans (1952) did not accept that these characters warranted recognition of *Pleurothyrium* as a genus. Kubitzki (1981) expressed the opinion that *Pleurothyrium* is a heterogenous genus and that its species actually belong to *Ocotea* and *Nectandra*. In contrast to this view, Rohwer & Kubitzki (1985) stated (based on a detailed analysis of *Ocotea* sens. lat.) that *Pleurothyrium* is a valid genus characterized by the lateral position of the locelli and the greatly enlarged glands. They pointed out that in *Pleurothyrium* only the inner three stamens (not all nine

TABLE 1. Distribution records of *Pleurothyrium* species.

| | |
|---|---|
| Bolivia | *P. intermedium, P. poeppigii* |
| Brazil | *P. acuminatum, P. amapaense, P. amplifolium, P. cuneifolium, P. insigne, P. intermedium, P. nobile, P. panurense, P. parviflorum, P. poeppigii, P. prancei, P. undulatum, P. vasquezii* |
| Colombia | *P. bracteatum, P. crassitepalum, P. cuneifolium, P. glabritepalum, P. grandiflorum, P. marginale, P. poeppigii, P. synandrum, P. tomiwahlii, P. trianae* |
| Costa Rica | *P. golfodulcense, P. hexaglandulosum, P. palmanum, P. pauciflorum, P. trianae* |
| Ecuador | *P. cinereum, P. cuneifolium, P. giganthum, P. glabrifolium, P. insigne, P. obovatum, P. parviflorum, P. poeppigii, P. tomentellum, P. tomiwahlii, P. trianae, P. williamsii* |
| Guatemala | *P. westphalii* |
| Honduras | *P. trianae* |
| Nicaragua | *P. trianae* |
| Panama | *P. hexaglandulosum, P. palmanum, P. pilosum, P. racemosum* |
| Peru | *P. acuminatum, P. bifidum, P. brochidodromum, P. cinereum, P. cuneifolium, P. insigne, P. intermedium, P. maximum, P. nobile, P. panurense, P. parviflorum, P. poeppigii, P. vasquezii, P. williamsii, P. tomentellum, P. trianae* |
| Venezuela | *P. amapaense, P. costanense, P. steyermarkianum, P. trianae* |

stamens) have glands at their base, thus accepting Nees's description and rejecting that of Mez and subsequent authors. Rohwer (1986) further discussed and illustrated this concept and accepted eight species groups in *Pleurothyrium*, based on a survey of the types of the published species. Van der Werff (1987, 1988) accepted the circumscription of *Pleurothyrium* given by Rohwer & Kubitzki (1985), as did Burger & van der Werff (1990); in these publications an additional five species are described. However, in recent British literature (Willis, 1973; Mabberley, 1987) only one species is attributed to *Pleurothyrium*; in all likelihood, these authors follow Bentham & Hooker (1880), who wrote that only one species matched Nees's description.

In this study I accept *Pleurothyrium* as a distinct genus, most closely related to *Ocotea* and *Nectandra*. It differs from these two genera in two easy to observe androecial characters. In *Pleurothyrium* the outer six stamens have at least two anther cells in a lateral position (and often all four are lateral), and the six staminal glands are strongly enlarged and always grow outward between the six outer stamens and separate these stamens. In many species the glands become confluent and form a large, pillowlike mass with the anthers embedded in the surface. Other characters that are uncommon or lacking in *Ocotea* and *Nectandra*, but frequently present in *Pleurothyrium*, are the position of the inflorescences in the axils of cataphylls (not or rarely in axils of normal leaves) and the presence of a marginal vein in the leaves. Whether *Ocotea* or *Nectandra* is the closest relative of *Pleurothyrium* is still an open question. This study has not pointed to a particular genus or species group as the closest relative.

Van der Werff (1991) published a key to the New World genera of Lauraceae, including *Pleurothyrium*.

Although the greatly enlarged and fused glands are unique among neotropical Lauraceae, they also occur in the Asian-Australian genus *Endiandra*. Several Australian species are illustrated in Hyland (1989). The enlarged, fused glands are about the only character *Pleurothyrium* and *Endiandra* have in common. *Endiandra* has only three two-celled stamens and does not have a cupule subtending the fruit; it is closely related to *Beilschmeidia*. Thus, the character of the glands is considered to be an example of convergence and does not indicate a close relationship.

## DISTRIBUTION AND ECOLOGY

*Pleurothyrium* species have been collected from Guatemala, the northernmost extension, to Bolivia and southern Brazil, the southernmost extension. It has been collected in all countries between these extremes with exception of El Salvador and the three Guianas. The genus is absent from the West Indies. Table 1 shows the species present in each country. The greatest concentration of species occurs in Peru, Brazil, Ecuador, and Colombia, while *Pleurothyrium* is represented by only a few species in the other countries. The Brazilian species are, with exception of *P. amplifolium*, Amazonian, and most occur in the upper part of the Amazon basin; only one or two species have been found downstream from Manaus. Most species are only known from lowland forests or the lower foothills of the Andes (below 1,000 m elevation). In Peru, *P. cuneifolium* and *P. poeppigii* occur at 1,800 m near Oxapampa, but these species are better represented in the lowlands. The Ecuadorian *P. obovatum* is only known from three collections at 1,200–1,800 m. In Venezuela, *P. costanense* has been collected

at 2,200 m, but is more common around 1,000 m; the poorly known *P. steyermarkianum* has been collected at 1,400 and 2,000 m.

Our knowledge about the habitat requirements of *Pleurothyrium* species is very poor. Older collections usually do not have habitat information other than "forest" and besides, many species are known from very few collections. For a reliable estimate of the habitat requirements, I would want at least ten collections with the same habitat information. This is only available for *P. parviflorum*, a species restricted to seasonally flooded forests in Peru, Brazil, and Ecuador. It is to be expected in the Amazonian forests of Colombia as well, but it has not yet been collected there. *Pleurothyrium panurense* is known from fewer collections, but all of these were made in flooded forest.

Most of the new or recently described species are from Colombia and Ecuador. For instance, six of the ten species from Colombia are new; for Ecuador these figures are seven out of twelve, but for Brazil it is two out of eleven species. Because of the Projeto Flora Amazonica, Amazonian Brazil has been reasonably well collected, probably better than Colombia, and it seems unlikely that many additional *Pleurothyrium* species will be collected in Brazil. On the other hand, Colombia has at least three additional, but incompletely known species. Taking this into consideration, I expect that the greatest diversity will be in Peru, Ecuador, and Colombia.

## Morphology and Taxonomic Characters

At the beginning of this survey of the taxonomic characters of *Pleurothyrium* species, it should be emphasized that about half of the species are known from only one or two collections. This is not enough for a good understanding of the morphological variation within the species, and there are difficulties interpreting differences in degree of pubescence, leaf size, and color of pubescence. Therefore, I decided not to recognize taxa based solely on these characters, even though, for instance, the Peruvian collection of *P. insigne* and the Costa Rican collection of *P. hexaglandulosum* look different from the types. Additional collections of many species are needed for a better understanding and, when available, may well lead to changes in the classification here proposed.

*Habit.* *Pleurothyrium* species vary from small to tall trees. There is no information about different types of tree architecture represented in the genus, but it is likely that species with clustered leaves have a different growth type than species with evenly spaced leaves.

*Habitat.* As with habit, label information on habitat is poor. The great majority of the species are restricted to the wet lowlands (below 500 m). *Pleurothyrium cuneifolium* and *P. poeppigii* have been found from the lowlands up to 1,800 m, an unusually wide range of altitude. *Pleurothyrium costanense* is restricted to cloud forest in Venezuela, between 800 and 2,200 m. *Pleurothyrium trianae* occurs occasionally up to 1,200 m, but is most common at elevations between 300 and 600 m. *Pleurothyrium palmanum* is known from four collections in Costa Rica and Panama, between 1,000 and 1,600 m. Finally, there are three montane species known from only three or fewer collections: *P. bracteatum* at 1,000 m in Colombia, *P. obovatum* at 1,200–1,800 m in southern Ecuador, and *P. racemosum* at 900 m in Panama. More detailed habitat preferences are only known for *P. panurense* and *P. parviflorum*: both are restricted to flooded forests in the upper Amazon basin. In the vicinity of Iquitos, Peru, I collected *P. parviflorum* in flooded forests on sandy and clay soils, but never found it outside flooded forests.

*Fistulose twigs.* Four species, *Pleurothyrium cuneifolium*, *P. obovatum*, *P. parviflorum*, and *P. poeppigii*, have consistently fistulose twigs, while *P. trianae* has rarely fistulose twigs. This is a reliable and readily visible character mentioned by Nees (1836b) in his descriptions. Mez (1889), citing Poeppig (In ramulis revera fistulosis degunt formicarum agmina pessime pungentia), referred to the ants living in the hollow twigs. On several, but certainly not all, labels of these species, the presence of aggressive ants is mentioned; I found *P. parviflorum* sometimes inhabited by aggressive ants and sometimes by timid ones, although each tree was inhabited by one kind only. In Lauraceae fistulose twigs inhabited by ants are not restricted to *Pleurothyrium*, but also occur in *Ocotea javitensis* (HBK) Pitt., *O. dendrodaphne* Mez, the species related to *O. atirrensis* Mez & J. D. Smith, including *Aiouea vextrix* van der Werff, a *Licaria* species from Costa Rica, and an *Aniba* species from Iquitos, Peru. Most Lauraceae with hollow twigs occur in the lowlands, but *P. obovatum*, known only from 1,800 m, has clearly hollow stems with exit holes. An undescribed *Ocotea* species from northern Ecuador, collected at 2,400 m elevation, also had hollow twigs inhabited by ants, as did an undescribed *Cinnamomum* species from central Ecuador, collected at 2,200 m elevation. Both high-elevation species were inhabited by non-aggressive ants, which did not defend the twigs and scarcely left the hollow core when the twigs were broken.

In *Pleurothyrium cuneifolium* and *P. poeppi-*

*gii*, the main axis of the inflorescences is not rarely fistulose. A good example is the type collection of *P. poeppigii*. These fistulose inflorescences tend to have very short lateral branchlets with the flowers rather densely fasciculate. In the past, all collections with this striking inflorescence shape were annotated as *P. poeppigii*, but floral characters show that this inflorescence shape also occurs in *P. cuneifolium*. In *Ocotea javitensis* the entire inflorescence can be reduced and carry a dense cluster of flowers; such specimens have also been identified as *Pleurothyrium* (for instance, *Klug 2908* as *P. densiflorum* Smith). Exactly how the activity of ants induces this peculiar inflorescence shape is not known to me.

*Leaf position.* Most species have alternate leaves, the predominant arrangement in Lauraceae. About ten species have the leaves clustered at the tips of the branches, potentially a useful character to separate species. However, I found this character not as useful as I hoped, because in some species the leaves are more or less clustered, and in some others the leaves are so large that an herbarium specimen consists of one leaf and an inflorescence and does not show the arrangement of additional leaves. Thus, I used leaf position in the key only when separating relatively small-leaved species.

*Leaf shape.* Leaf shape ranges from elliptic to strongly obovate. In most species it is rather stable, but I found it difficult to express leaf shape accurately in words and have not used it very much in the key. A few striking leaf shapes should be mentioned: in *Pleurothyrium maximum*, *P. insigne*, and *P. williamsii* the leaves are gradually narrowed toward the base and at the base are abruptly rounded to cordate; in *P. racemosum* and *P. pilosum* the leaves are obtuse or rounded both at the base and apex. *Pleurothyrium tomiwahlii* has a similar leaf shape, but the base is sometimes acute, not obtuse.

*Leaf venation.* Leaf venation includes both camptodrome and brochidodrome types as well as their intermediates. All species with small flowers and free staminal glands (the first eleven species in the key) have predominantly camptodrome venation, while the species with larger, rotate flowers have camptodrome or brochidodrome venation. Leaf size or shape does not seem to affect venation type strongly; some species with large, obovate leaves have a strongly developed marginal vein (*Pleurothyrium insigne*, *P. maximum*), but others (*P. tomiwahlii*, *P. giganthum*) do not. Among the species with small leaves, *P. marginale* has a strong marginal vein, but *P. golfodulcense*, *P. glabritepalum*, and *P. westphalii* do not have a marginal vein. Although venation type seems characteristic for each species, the various types are hard to describe accurately and have not been used much in the key. A detailed study of the venation types of *Pleurothyrium* is in preparation and will be published separately.

*Indument.* The type of indument is a very useful character for identification. Because indument on leaves and twigs can be different, I have mostly used the indument on the lower leaf surface, in which I recognize three types. A little more than half the species have glabrous leaves or carry a sparse, appressed indument, which never covers the entire lower surface. A group of ten species has erect straight or tortuous (in *Pleurothyrium racemosum*) hairs, which never cover the entire surface and which, in some species, can be sparse. The third group has a dense (mostly tomentose) pubescence, which completely covers the lower leaf surface. With the exception of three species (*P. crassitepalum*, *P. panurense*, and *P. tomiwahlii*), these pubescence types can easily be recognized. In the three exceptions, it is sometimes difficult to choose between group one (glabrous or sparse, appressed pubescence, the surface visible) or group three (dense pubescence, covering the entire surface). These species are therefore included twice in the key. The three groups based on pubescence types are not natural; sometimes closely related species (for instance, *P. insigne-P. maximum*) are placed in different groups. These groups are formed solely to allow easy identification.

*Inflorescences.* Inflorescences of *Pleurothyrium* are as a rule thyrso-paniculate in the sense of Weberling (1985). They consist of a central axis with a number of alternately positioned lateral axes. The lateral axes are once to several times cymosely branched; the central flower of each cyme flowers before the lateral ones and is usually absent in all but the terminal cymes. Of each cyme, the lateral elements may again be cymosely divided, but the central element always develops into a single flower. Sometimes the lateral elements of the lateral branches fail to develop and then the inflorescence is racemose (as in *P. racemosum*).

In most species inflorescence bracts are early deciduous and absent at anthesis. Exceptions are *Pleurothyrium bracteatum* and *P. golfodulcense*, both of which have rather large bracts at anthesis.

The thyrso-paniculate inflorescence type is very common among neotropical Lauraceae and occurs in all larger genera, such as *Ocotea*, *Nectandra*, *Persea*, *Aniba*, *Licaria*, *Aiouea*, *Endlicheria*, and *Cinnamomum*.

In general, the inflorescences are found in the axils of cataphylls just below the terminal bud.

Although they appear terminal, I have always found them to be lateral. In the species group characterized by erect tepals, inflorescences occur occasionally in the axils of regular leaves, but this is uncommon. In *Pleurothyrium giganthum*, the inflorescences are inserted in the axils of cataphylls below the leaves. However, many species are represented by very few collections and I am not certain that the position of the inflorescences, below or above the leaves, is of any significance.

The nearly consistent presence of inflorescences in the axils of cataphylls is a helpful character for the identification of *Pleurothyrium*. The great majority of species of *Ocotea* and *Nectandra* have inflorescences in the axils of normal leaves, but such species as *O. fasciculata* (Nees) Mez and *N. megapotamica* (Spreng.) Mez are exceptions.

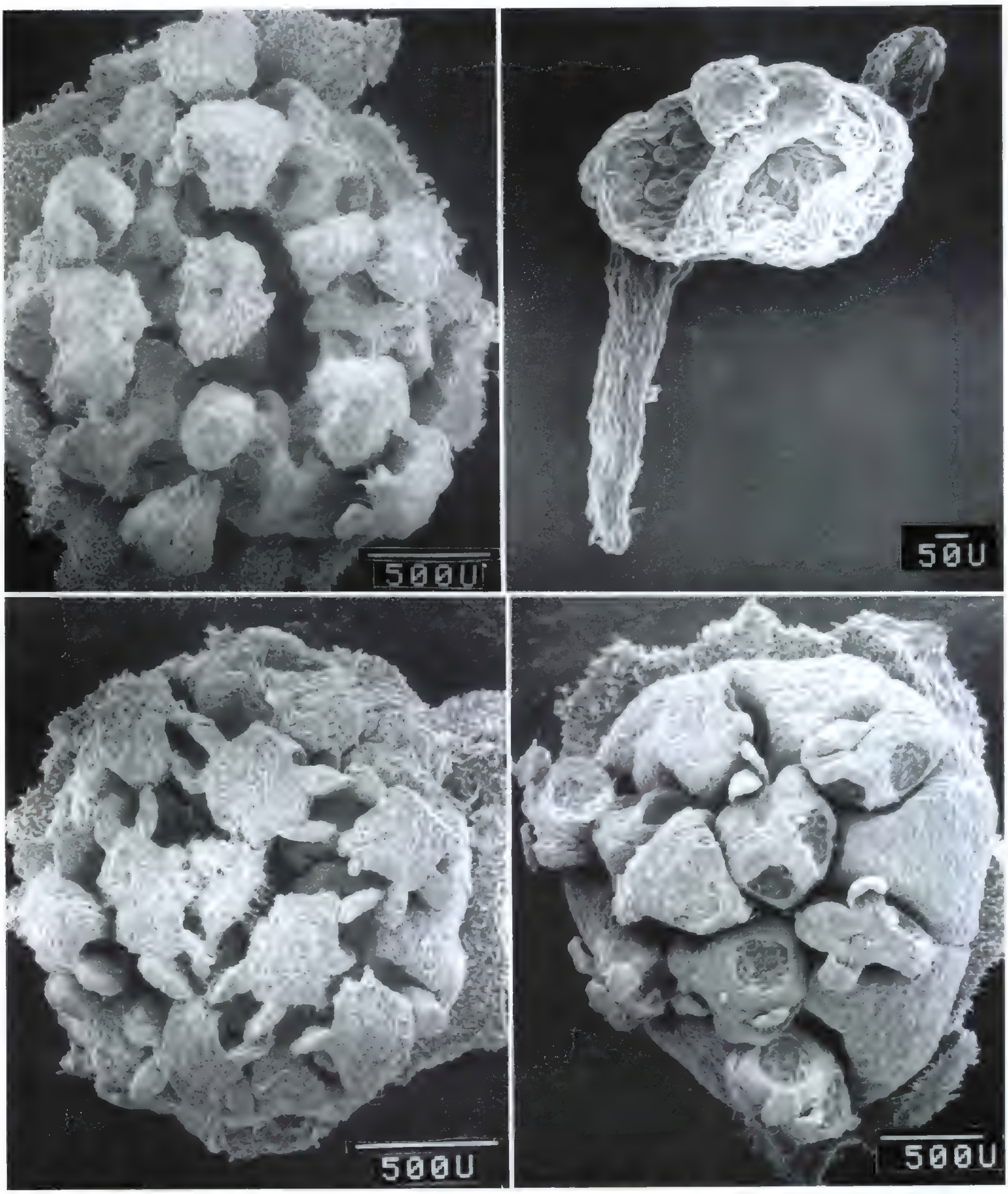
*Flowers.* The flowers offer a number of discriminating and/or interesting characters. Eight species have more or less erect tepals at anthesis, this in contrast to the remaining species, which have a rotate flower shape. Six of these eight (the exceptions are *Pleurothyrium acuminatum* and *P. amapaense*) also have reflexed margins of the tepals. These reflexed margins are not a result of aging of the flowers; I have seen *P. parviflorum* and *P. trianae* in the field and even young flowers have reflexed margins of the tepals. On herbarium sheets one can see that sometimes buds have already reflexed margins of the tepals. I consider the species with erect tepals, together with *P. cuneifolium* and *P. obovatum*, a closely related group, characterized by flower shape, absence of a marginal vein, similar indument on the pistil, occurrence of fistulose stems, and the rather slender tepals.

Most other species have rotate flowers and broadly ovate to roundish tepals. Species with flowers more than 10 mm in diameter show a tendency toward unequal tepals, with the inner tepals slightly shorter and narrower than the outer ones. The group of species with erect tepals always has equal tepals. In one species, *Pleurothyrium tomiwahlii*, the tepals are strongly reflexed at anthesis and become parallel to the pedicel in older flowers.

The pubescence on the outside of the tepals is frequently much denser or longer on the areas exposed to the outside in bud than on areas protected from the outside. Thus, the outer three tepals and a basal, triangular patch on the inner tepals have a similar pubescence. This is an unusual character in Lauraceae, but is fairly common in the group of species with rotate flowers. It does not occur in the group of species with erect tepals.

The pubescence on the inside of the tepals is variable and is a useful character in separating the taxa. A few species (*Pleurothyrium cuneifolium*, *P. glabrifolium*, *P. glabritepalum*, *P. panurense*, and *P. prancei*) have a glabrous inner surface of the tepals (in *P. prancei* the outer three are glabrous inside, the inner three papillose). Occasionally, some scattered papillae or hairs may be present, especially near the base of the tepals, but a homogeneous cover of papillae or hairs is lacking. The group of species with pubescent inner surfaces of the tepals is also small; it includes *P. bracteatum*, *P. giganthum*, *P. crassitepalum*, *P. tomiwahlii*, *P. grandiflorum*, *P. marginale*, *P. pilosum*, and *P. westphalii*. In *P. racemosum* the inner tepals are pubescent and the outer three have a large, triangular, pubescent patch at the base and are otherwise papillose. The remaining species all have a papillose inner surface.

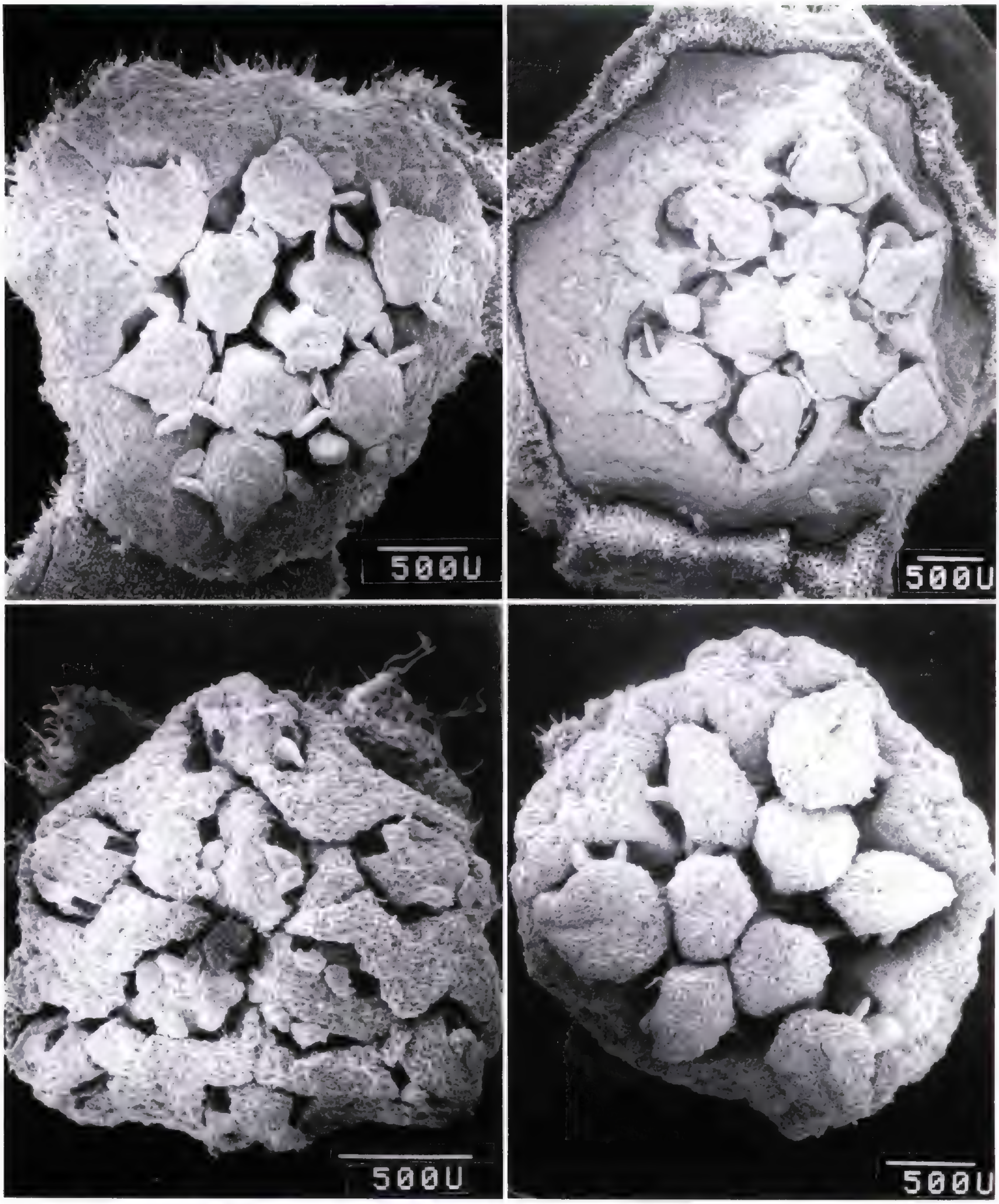
The different androecial configurations are the most interesting feature of *Pleurothyrium*. In the group of species with erect tepals the enlarged glands grow outward, and the six outer stamens are separated from each other by the glands (Fig. 1). In this flower type the glands do not grow around the outer anthers, and the glands do not touch each other at the periphery of the flower. The stamens have relatively long filaments and the anther cells occupy nearly the entire anther (Fig. 2). The anther is somewhat curved inward, but not horizontal; thus, the anther cells are arranged in an upper and lower pair. The lower pair is always toward the outside in relation to the upper pair. Because of the long filaments, the anthers are clearly raised above the glands. In the next stage, the glands begin to enclose the outer stamens, while the anthers become horizontal, have lateral anther cells, and are not raised above the glands. An example is *P. vasquezii* (Fig. 3). In other species the glands completely surround the outer stamens and appear to form a wall around the stamens. The contact lines between the glands are sometimes clearly visible (Fig. 4) or almost disappear (Fig. 5). In the final stage all stamens are crowded in the center of the flower, surrounded by a broad wall of completely fused glands (Fig. 6). The enlarged glands do not confine the stamens to the center of the flower in all species. In some species the glands grow between the stamens and separate them, especially the stamens of the second whorl (Fig. 7). This configuration is not common; it occurs in *P. golfodulcense*, *P. cinereum*, *P. tomiwahlii*, *P. crassitepalum*, and *P. racemosum*. The species with this flower type also tend to have stamens and




FIGURES 1–4.—1. (Top left.) Flower of *Pleurothyrium poeppigii*, tepals removed (*Palacios 2775*).—2. (Top right.) Stamen (Whorls I–II) of *P. acuminatum* (*van der Werff 9967*).—3. (Bottom left.) Flower of *P. vasquezii*, tepals removed (*Vasquez 7889*).—4. (Bottom right.) Flower of *P. tomentellum*, tepals removed (*Gudiño 12*).

glands forming a taller "dome"; this dome can be as high as its width. In *P. tomiwahlii* the dome is also seated on a short column, thus further raising the androecium. All species with horizontally bent anthers and glands that are (nearly) enclosing the outer stamens have rotate flowers. These species have, on the average, distinctly larger flowers than the species with erect tepals. Unfortunately, no data on pollination are available, but it seems likely that the species with large, rotate flowers are pollinated by different organisms than those with small flowers with erect tepals.

The indument of the pistil shows considerable variation. Sixteen species were found to have the pistil more or less covered with papillae. Often the lower part of the ovary was glabrous and the density




FIGURES 5–8.—5. (Top left.) Flower of *P. insigne*, tepals removed (*Palacios 4388*).—6. (Top right.) Flower of *P. grandiflorum*, tepals removed (*Juncosa 1675*). —7. (Bottom left.) Flower of *P. golfodulcense*, tepals removed (*Jimenez 648*).—8. (Bottom right.) Flower of *P. brochidodromum*, tepals removed (*Vasquez 7865*).

of the papillae decreased also on the style, but papillae were easily seen on the upper part of the ovary. This condition is present in all species with erect tepals, as well as in *Pleurothyrium bifidum*, *P. brochidodromum*, *P. nobile*, *P. palmanum*, *P. panurense*, *P. vasquezii*, and *P. williamsii*. Ten species have a glabrous pistil: *P. tomiwahlii*, *P. crassitepalum*, *P. glabrifolium*, *P. glabritepalum*, *P. grandiflorum*, *P. marginale*, *P. pilosum*, *P. racemosum*, *P. giganthum*, and *P. westphalii*. The remaining species have a (partly) pubescent pistil. In a few species one finds six bald spots on the upper part of the pubescent ovary corresponding to the contact points between the six glands and the ovary. I have not used the indument of the pistil frequently in the key, because the pu-

bescence is only readily visible on the style in a few species.

Fruits and cupules are unknown for many species. When known, the cupules are relatively deeply cup-shaped and have nearly always conspicuous lenticels or warts. Because of the deep cupules, fruiting collections have sometimes been misidentified as *Aniba* sp., but venation (*Pleurothyrium* has in general more lateral veins and sometimes a distinct marginal vein) and indument (ferruginous tomentum is a good indication for *Pleurothyrium*) help separate the two genera. Frequently, the tepals are persistent on the young cupules. The tepals eventually become damaged and break off or the growing cupule causes the tepals to fall off. In this character, *Pleurothyrium* species differ from *Nectandra*, where the tepals tend to be basally united and fall off as a unit, together with the stamens. Unusual characters are the presence of six large lobes on the cupules of highland populations of *P. poeppigii* in the Selva Central in Peru; the common name "roble zapallo" alludes to this (zapallo = squash). Young cupules of *P. giganthum* are sharply hexangular, a feature not found in other species. In *P. cinereum* the tepals are persistent on the mature cupule, which may be double-rimmed.

*Pollen.* In a survey of pollen types of neotropical Lauraceae, Raj & van der Werff (1988) found that, with the exceptions of *Cryptocarya* and *Cassytha*, all investigated species had inaperturate, spinulose pollen grains. Pollen of *Pleurothyrium* was found to be very similar to that of *Ocotea*, the main differences being size and ultrastructural details of the sporoderm. Pollen of *Nectandra* is more distinct. Three species of *Pleurothyrium* (*P. parviflorum*, *P. trianae*, and *P. cuneifolium*) were included in this study. Because these three species belong to the group with erect tepals and erect or curved anthers, I checked pollen of two species with rotate flowers and bent anthers (*P. insigne* and *P. racemosum*). These two species have the same inaperturate, spinulose pollen that is present in nearly all neotropical Lauraceae. Because all five investigated *Pleurothyrium* species have the same pollen type, it seems unlikely the pollen will be useful in the classification of *Pleurothyrium* species, and pollen of the other species has not been studied.

## Cladistic Analysis

A cladistic analysis, based on the principles of phylogenetic systematics as developed by Hennig (1966), was made of *Pleurothyrium*, using the 39 species recognized in this revision as terminal taxa. Because several species of *Pleurothyrium* are still poorly known, the choice of characters to be used in the analysis was limited to those characters visible on a herbarium sheet. Ideally, one wishes for characters from other fields (such as embryology, anatomy, chemistry) as well as more characters. The characters and the character states used are listed in Table 2; the data matrix is presented in Table 3. The choice of outgroup, and therefore also the polarity of the character states, initially posed considerable problems. Of all genera of Lauraceae, *Nectandra* and *Ocotea* are the closest to *Pleurothyrium*, based on overall morphology. However, neither of the two seems closer to *Pleurothyrium* than the other. Because *Ocotea* and *Nectandra* are very similar in the character states used in this analysis, which of them was chosen as the outgroup seemed relatively unimportant, thus a preliminary analysis was made with the generic concept of *Nectandra* as outgroup. This analysis resulted in 1,988 trees; after successive weighting 293 trees were generated. A strict consensus tree showed as the most derived group of species those species with erect tepals and free, weakly enlarged glands. This topology ran completely counter to my ideas of trends within *Pleurothyrium*. Based on knowledge gained from my nine years of studying Lauraceae, I consider the following character states in *Pleurothyrium* as primitive: free, weakly enlarged glands, stamens with only two of the four anther cells lateral and the anthers raised well above the glands, the occasional presence of inflorescences in the axils of normal leaves, the absence of a marginal vein, and erect tepals. As derived character states, I regard fused, strongly enlarged glands, stamens with four lateral anther cells, anthers that are not or scarcely raised above the glands, inflorescences strictly in the axils of cataphylls, presence of a marginal vein and spreading, rotate (or even reflexed) tepals. These ideas on primitive and derived characters in *Pleurothyrium* are based on my extensive experience with neotropical Lauraceae. Because *Nectandra* and several hermaphroditic species of *Ocotea* (including most South American *Ocotea* species with perfect flowers) have flowers with spreading tepals, the *Pleurothyrium* species with erect tepals ended up as derived in the phylogenetic tree. There are some *Ocotea* species with perfect flowers and erect tepals (for instance, the *O. insularis* group), but various reasons (entirely different indument of anthers, presence of flattened branchlets of inflorescence) make it highly unlikely that *O. insularis* can be considered as outgroup for *Pleurothyrium*.

TABLE 2. Characters and character states used in cladistic analysis of *Pleurothyrium*.

| | |
|---|---|
| 1. Position of tepals | 0 = spreading<br>1 = erect |
| 2. Margin of tepals | 0 = plane<br>1 = inrolled |
| 3. Marginal vein | 0 = lacking<br>1 = present |
| 4. Indument on inner surface of tepals | 0 = glabrous<br>1 = papillose<br>2 = pubescent |
| 5. Indument of pistil | 0 = glabrous<br>1 = papillose<br>2 = pubescent |
| 6. Indument of floral tube | 0 = glabrous<br>1 = papillose<br>2 = pubescent |
| 7. Glands | 0 = free, not surrounding stamens<br>1 = surrounding stamens, ± fused |
| 8. Stamens | 0 = adjacent<br>1 = separated from each other by glands |
| 9. Twigs | 0 = solid<br>1 = fistulose |
| 10. Number of lateral veins | 0 = 5–9<br>1 = 10–15<br>2 = 16 or more |
| 11. Tepals | 0 = equal<br>1 = subequal |
| 12. Position of leaves | 0 = alternate<br>1 = clustered |
| 13. Pubescence on lower leaf surface | 0 = glabrous or appressed<br>1 = erect |
| 14. Position of inflorescence | 0 = in axils of leaves<br>1 = in axils of bracts |
| 15. Position of anther cells | 0 = 2 lateral<br>1 = 4 lateral |
| 16. Pubescence of bracts | 0 = only on outer surface<br>1 = on inner and outer surface |

Character states of 4, 5, 6, and 10 are unordered.

A second analysis was made with a primitive species of *Pleurothyrium*, *P. acuminatum*, as outgroup. This species was chosen because it lacks the derived characters listed earlier, and it also lacks fistulose twigs and has plane, not inrolled, tepal margins. Analysis of the data matrix using the MHennig* and bb* Wagner parsimony options of Hennig86 (Farris, 1988) produced 540 most parsimonious trees (length 79 steps, consistency index 0.25). A strict consensus tree based on these 540 trees showed an alphabetical listing of 32 species, with only seven species slightly better resolved. The successive weighting procedure on the 540 trees resulted in at least 1,149 trees (overflow) with a length of 110 steps and a consistency index of 0.50. Note that the high value for the length is a function of the weight being scaled up to a value of 10. Although most characters were weighted after the successive weighting procedures, four of the sixteen characters (10, 11, 13, and 14) weighted zero. The analysis was repeated without those characters and resulted in 230 most parsimonious trees with a length of 44 steps and a consistency index of 0.34. After successive weighting, the analysis produced 118 trees with a length of 98 steps and a consistency index of 0.58. As a consequence of deleting the four "weightless" characters, the analysis resulted in a smaller number of trees with fewer steps and a higher consistency index: these four characters must have contributed a great deal of homoplasy to the first analysis.

A strict consensus tree based on the 118 trees of the second analysis is presented in Figure 9a, while one of the 118 equally parsimonious trees, selected at random, is presented in Figure 9b. The following comments apply to both cladograms. The changes in character states throughout the cladogram are added to the tree. In both cladograms, the species group I consider primitive forms the basal group. The second, largest group is not well

TABLE 3. Data matrix for cladistic analysis.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Nectandra | ? | 0 | 0 | 1 | ? | ? | 0 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 1 | ? |
| acuminatum | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| amapaense | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| amplifolium | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ? |
| bifidum | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | ? | 0 | 1 | 1 | 1 | 0 |
| bracteatum | 0 | 0 | 1 | 2 | 2 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 1 |
| brochidodromum | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 1 |
| cinereum | 0 | 0 | 0 | 1 | 2 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 |
| costanense | 0 | 0 | 1 | 1 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 |
| crassitepalum | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | ? |
| cuneifolium | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | ? | 0 | 0 | ? | 0 | 0 | 1 |
| giganthum | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 |
| glabrifolium | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | ? | 1 | 1 | 0 |
| glabritepalum | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | ? |
| golfodulcense | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 |
| grandiflorum | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | ? |
| hexaglandulosum | 0 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | ? |
| insigne | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 1 | 1 | 0 |
| intermedium | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| marginale | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | ? | 1 | 0 | 0 | 1 | 1 | ? |
| maximum | 0 | 0 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | ? | 1 | 0 | 0 |
| nobile | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 |
| obovatum | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | ? | 1 | 0 | ? |
| palmanum | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 |
| panurense | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 |
| parviflorum | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| pauciflorum | 0 | 0 | 1 | 1 | 2 | 2 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 1 |
| pilosum | 0 | 0 | 0 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | ? | 1 | 1 | 1 | 1 | ? |
| peoppigii | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 1 |
| prancei | 0 | 0 | 1 | 0 | 2 | 2 | ? | 0 | 0 | 1 | 1 | 0 | ? | 1 | 1 | 0 |
| racemosum | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 |
| steyermarkianum | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 |
| synandrum | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 |
| tomentellum | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 |
| tomiwahlii | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 |
| trianae | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| undulatum | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| vasquezii | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| westphalii | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? |
| williamsii | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 1 |

resolved; the large number of trees before constructing the consensus tree reflects variation in topology in this group. The cladograms include only four synapomorphies (for characters 1, 2, 7, and 10), indictaing that all other changes are changes in unordered states or homoplasies. Although nearly all cladograms include some amount of homoplasy, to have a cladogram for 39 terminal taxa with only four synapomorphies suggests that the data needed for a cladistic analysis were not available.

Reviewing this attempt at making a phylogenetic classification as a byproduct of a taxonomic revision of *Pleurothyrium*, one may note several problems. First, the number of characters is much lower than the number of terminal taxa. Second, the poor understanding of relationships within Lauraceae makes the choice of an outgroup somewhat arbitrary, and therefore the choice of polarity of the character states cannot be defended very well. Because the choice of outgroup influences the classification strongly, the cladogram cannot be any more reliable than the choice of outgroup. Third, the phylogenetic classification is entirely based on gross morphological characters of herbarium specimens. These characters were not selected because

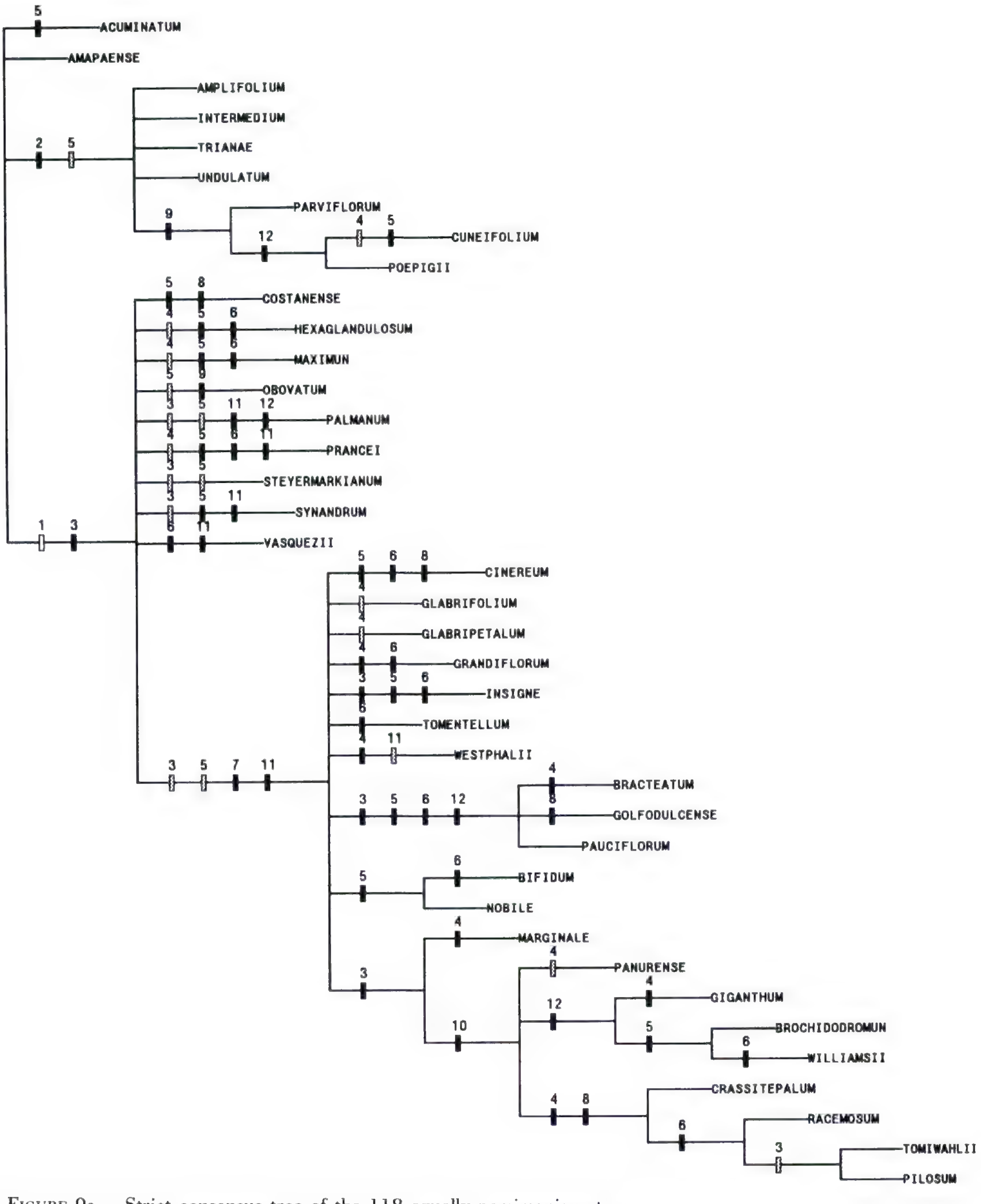



FIGURE 9a. Strict consensus tree of the 118 equally parsimonious trees.

they were regarded as good indicators of phylogenetic relationships, but because they were all that was available. Ideally, one wishes for characters that are regarded as good indicators of phylogenetic relationships. In reality, one does not have much choice about quantity and quality of characters when 19 of the 39 terminal taxa are known from only one or two collections.

In general, a taxonomic classification of a group requires the data needed for the circumscription and identification of the taxa involved. For a phylogenetic classification one needs, in addition to the data for a taxonomic classification, also data showing the evolution within the group over time. Or, to phrase it differently, a phylogenetic classification contains more information than a taxonomic clas-

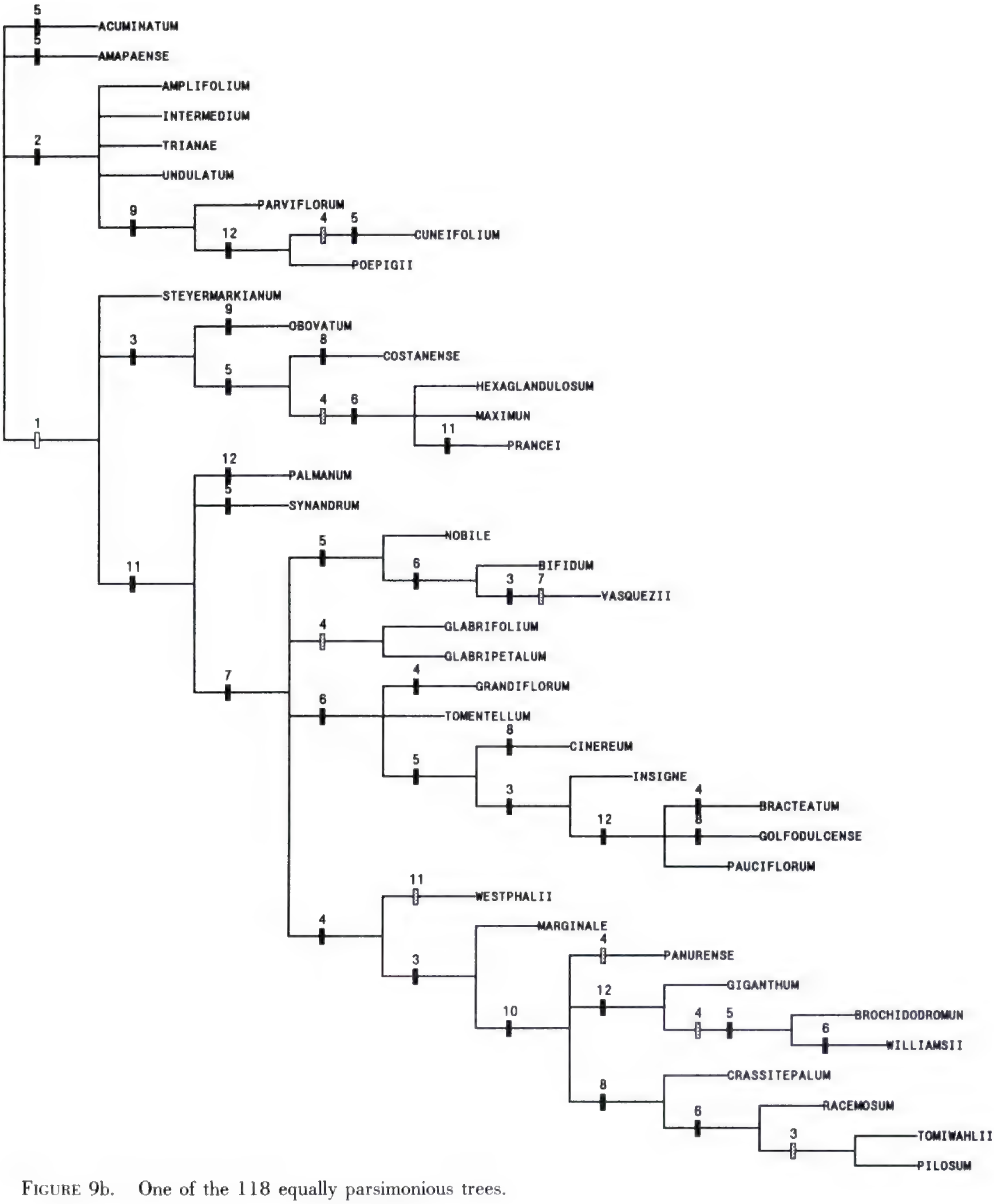



FIGURE 9b. One of the 118 equally parsimonious trees.

sification, and consequently requires a larger input of information. In the case of *Pleurothyrium*, sufficient information is available for taxonomic revision, but not enough for a phylogenetic classification. Obtaining sufficient information for a proper phylogenetic analysis is a project unto itself and making a phylogenetic analysis cannot be merely tacked on to making a taxonomic revision.

Relationships between *Pleurothyrium* species as expressed in the cladogram and as based on morphological similarities show some congruence. For instance, I consider *P. racemosum*, *P. tomiwahlii*, and *P. pilosum* as closely related, a relationship expressed in all cladograms inspected. Likewise, the species with erect tepals, usually with inrolled margin of the tepals, are closely related, as shown

in the cladograms; I would also include *P. obovatum* in this group, a species placed in the more advanced group in the cladograms. Other pairs of closely related species (at least in my opinion) placed well apart in the consensus tree are *P. insigne* and *P. maximum* and, to a lesser degree, *P. costanense* and *P. synandrum*, as well as *P. westphalii* and *P. grandiflorum*.

## Species Concept

In preparing this treatment, it was necessary to deal with the number of published species whose distinctiveness was less than convincing. In some cases ample recent collections made it clear that certain taxa (for instance, *P. reflexum* and *P. zulianense*) had to be synonymized. In other cases such collections were not available. In these instances I let myself be guided by the principle to only change the status quo if there was a strong reason for doing so. This means that some species whose distinctiveness I doubt are being maintained (examples are *P. amplifolium*, *P. undulatum*, *P. amapaense*, and *P. intermedium*) and that other taxa, represented by, in my opinion, inadequate collections, are not being described. My reasons for not describing these taxa are twofold: (a) incomplete descriptions make identification of future, complete collections very difficult; (b) the absolute certainty that specimen X (sterile or in fruit) represents an undescribed species of genus A can turn a few weeks later into nagging doubt.

## Typification

Botanists who described species of *Pleurothyrium* in the nineteenth century never designated holotypes. Usually they cited only a type collection, often indicating in which herbaria they had seen duplicates of the type collection. When only one specimen was cited, I have regarded this as the holotype, even though it was not explicitly annotated as such. If several duplicates exist of the type collection, I have listed them as syntypes. In all cases the syntypes I have seen belonged to the same species, and there cannot be any confusion about the application of the names in question. For this reason it seemed unnecessary to designate lectotypes, and I have therefore not selected lectotypes. Another reason not to select lectotypes is that I very likely have not seen all the existing syntypes, as required by the Code. For instance, I have not seen the specimens at P, and I have no doubt that syntypes of some species are present in other herbaria I did not consult. Lectotypification would be advisable if two or more collections are cited as types of a given species, but this is not the case for any *Pleurothyrium* species.

## Taxonomic Section

**Pleurothyrium** Nees, in Lindley, Nat. Syst. Bot.: 422. 1836. *Ocotea* sect. *Pleurothyrium* (Nees in Lindley) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. *Ocotea* subg. *Pleurothyrium* (Nees in Lindley) Kostermans, Comm. Forest Res. Inst. 57: 40. 1957. TYPE: *Pleurothyrium chrysophyllum* Nees (lectotype, selected by Kostermans, 1952).

Trees. Twigs solid or in a few specimens fistulose and inhabited by ants. Leaves alternate or clustered near the tips of branches, mostly elliptic or obovate; venation camptodrome or brochidodrome. Inflorescences in axils of cataphylls, rarely in axils of normal leaves, thyrso-paniculate, rarely by reduction racemose, the ultimate divisions cymose. Flowers rotate at anthesis or in some species with erect tepals. Tepals 6, equal or subequal, then with the inner three a little narrower and shorter. Fertile stamens 9, all 4-celled, the outer 6 with the anthers curved inward or sharply bent inward, the cells mostly lateral, sometimes 2 cells extrorse or introrse; inner three anthers mostly curved outward, with lateral cells. Staminodia frequently present, but small and inconspicuous. Filaments of the inner three stamens each with two glands near the base, these strongly enlarged and growing outward, sometimes fused and enclosing the outer stamens and the anthers embedded in the glandular tissue. Pistil glabrous, papillose or pubescent, largely immersed in the receptacle. Cupule usually deeply cup-shaped, conspicuously warty. Fruit a one-seeded drupe.

## Key to the Species of *Pleurothyrium*

| | | |
|---|---|---|
| 1 | Twigs fistulose | 2 |
| 1. | Twigs solid | 6 |
| 2(1). | Flowers rotate, 7–14 mm diam.; tepals glabrous or papillose on inner surface | 3 |
| 2. | Tepals ± erect at anthesis, flowers ca. 5 mm diam., tepals papillose on inner surface | 4 |
| 3(2). | Terminal buds, inflorescences, and flowers ferruginous-tomentellous; leaves glabrous below | *P. obovatum* |
| 3. | Indument, when present, brown; leaves mostly papillose or tomentellous below, rarely glabrous | *P. cuneifolium* |
| 4(2). | Twigs, inflorescences, and flowers glabrous or minutely puberulent | *P. parviflorum* |
| 4. | Twigs, inflorescences, or flowers papillose or tomentellous | 5 |

5(4). Lateral veins 14–18 on each side; leaves firmly chartaceous to subcoriaceous; always with fistulose twigs ..... *P. poeppigii*
5. Lateral veins 8–12; leaves chartaceous; rarely with fistulose twigs ..... *P. trianae*
6(1). Tepals at anthesis erect and sometimes twisted, the margins usually reflexed; staminal glands free, never coalesced; diameter of flowers 5 mm or less; marginal vein lacking, lower leaf surface never with erect hairs ..... 7
6. Tepals at anthesis rotate, plane, the margins not reflexed; staminal glands free or coalesced; diameter of flowers equal to or greater than 8 mm (in *P. glabrifolium*, *P. vasquezii*, and *P. tomentellum* flowers 5–8 mm diam.); marginal vein present or absent, in some species lower leaf surface with erect hairs ..... 12
7(6). Leaves ± clustered at tips of branches; pubescence on inflorescences and young twigs ferruginous-tomentellous ... *P. amapaense*
7. Leaves alternate, not clustered; pubescence on inflorescence and young twigs gray or (light) brown, never ferruginous ..... 8
8(7). Margin of tepals not reflexed; tepals ± twisted at anthesis; leaf apices acuminate ..... *P. acuminatum*
8. Margin of tepals reflexed; tepals not twisted; leaf apices acute ..... 9
9(8). Twigs and inflorescence axes sparsely pubescent; flowers and terminal bud much more densely pubescent ..... *P. intermedium*
9. Degree of pubescence on flowers and terminal bud similar as on inflorescence axes and twigs ..... 10
10(9). Flowers subsessile, the pedicels shorter than the flowers ..... *P. undulatum*
10. Flowers with pedicels as long as or longer than the flowers ..... 11
11(10). Petioles 8–14 mm long; filaments of stamens longer than anthers, clearly visible in old flowers; leaves 7–10 cm wide; known only from Rio de Janeiro ..... *P. amplifolium*
11. Petioles 10–20 mm long; filaments as long as or shorter than anthers, scarcely exceeding glands and not readily visible in old flowers; leaves usually narrower than 8 cm; northern South America ..... *P. trianae*
12(6). Lower leaf surface tomentose or tomentellous, the leaf surface completely hidden by the indument ..... 13
12. Lower leaf surface glabrous or sparsely pubescent, the leaf surface never completely hidden ..... 20
13(12). Indument of lower leaf surface whitish, very short, the individual hairs scarcely visible 14
13. Indument of lower leaf surface brown or ferruginous, very short or longer and then individual hairs visible ..... 15
14(13). Inner surface of tepals glabrous; inflorescences 5–10 cm long; leaves 15–30 cm long ..... *P. panurense*
14. Inner surface of tepals papillose; inflorescence 15–25 cm long; leaves 30–40 cm long ..... *P. bifidum*
15(13). Bracts to 1 cm long present on inflorescence during anthesis; marginal vein present; pubescence on young twigs and inflorescence reddish brown ..... *P. bracteatum*
15. Bracts generally lacking on inflorescences at anthesis (if present, small); marginal veins lacking or present; pubescence on inflorescence brown or yellow-brown ..... 16
16(15). Lateral veins 18–24; leaves generally widest below the middle ..... *P. synandrum*
16. Lateral veins to 15–16; leaves widest at or above the middle ..... 17
17(16). Tepals subequal, the inner three shorter and narrower than the outer three, both inner and outer surface pubescent; marginal vein present ..... *P. crassitepalum*
17. Tepals equal, the inner surface papillose or puberulous; marginal vein weakly developed or lacking ..... 18
18(17). Flowers 10–12 mm diam. ..... 19
18. Flowers to 8 mm diam. ..... *P. tomentellum*
19(18). Style gray-pubescent; receptacle pubescent inside; indument of lower leaf surface ± appressed, the hairs very short ..... *P. cinereum*
19. Style papillose; receptacle glabrous inside; indument of lower leaf surface tomentellous, the hairs ± erect, curled ... *P. palmanum*
20(12). Lower leaf surface with erect hairs, this indument sometimes sparse ..... 21
20. Lower leaf surface glabrous or with appressed hairs ..... 30
21(20). Leaves obovate or oblong-obovate, 20–60 cm long, the marginal vein strongly developed from near the base to the apex ..... *P. insigne*
21. Leaves obovate or elliptic (in *P. racemosum* oblong, but less than 15 cm long), a marginal vein lacking or only present in the distal half of the leaf ..... 22
22(21). Leaves 30–60 × 15–24 cm, obovate, clustered, marginal vein lacking or weakly developed; flowers large, ca. 2 cm diam. ..... *P. giganthum*
22. Leaves smaller and narrower, alternate or clustered, marginal vein sometimes present; flowers less than 15 mm diam. ..... 23
23(22). Tepals reflexed at anthesis; androecium situated on top of a short, pubescent column; pubescence on lower leaf surface sparse; leaves obovate, clustered ..... *P. tomiwahlii*
23. Tepals spreading at anthesis; androecium never raised on a short column; pubescence on lower leaf surface visible; leaves elliptic, oblong, or obovate, alternate or clustered 24
24(23). Leaf base and apex obtuse or rounded ..... 25
24. Leaf base and apex not both obtuse or rounded, usually at least apex acute or acuminate ..... 26
25(24). Leaves 15–25 cm long, densely pilose below ..... *P. pilosum*
25. Leaves 6–14 cm long, glabrescent with age, indument persisting longest near the base along margin and veins ..... *P. racemoseum*
26(24). Inflorescences few-flowered (± 7 flowers per inflorescence), 2–5 cm long ..... 27

26. Inflorescences with (many) more than 7 flowers, (8–)10–25 cm long ..... 28
27(26). Flowers ca. 8 mm diam., tepals half-erect; leaves 16–35 cm long; ovary and receptacle pubescent ..... *P. pauciflorum*
27. Flowers ca. 13 mm diam.; tepals spreading; leaves 10–18 cm long; ovary and receptacle glabrous ..... *P. glabritepalum*
28(26). Pistil pubescent; pubescent style easily visible above the androecium ..... *P. costanense*
28. Pistil papillose; style not pubescent ..... 29
29(28). Flowers 5–6 mm diam.; leaves alternate ..... *P. vasquezii*
29. Flowers 9–10 mm diam.; leaves ± clustered ..... *P. brochidodromum*
30(20). Inner surface of tepals glabrous (in *P. prancei* only larger, outer three tepals; inner, smaller ones are papillose) or with a few small lines of papillate hairs ..... 31
30. Inner surface of tepals uniformly pubescent or papillose-pubescent ..... 34
31(30). Leaves 30–50 cm long, the base abruptly rounded or cordate; inflorescences 40–65 cm long ..... *P. maximum*
31. Leaves 10–30 cm long, the base acute or obtuse; inflorescences to 20 cm long ..... 32
32(31). Leaves clustered at tips of branches; lower leaf surface with minute, appressed, whitish indument, thus lower and upper leaf surface markedly discolorous; inundated forests ..... *P. panurense*
32. Leaves not clustered; upper and lower leaf surface not or scarcely discolorous ..... 33
33(32). Inner tepals papillose inside, shorter and narrower than the outer ones, these glabrous inside; inflorescence tomentose ..... *P. prancei*
33. All tepals equal in shape and glabrous inside; inflorescence tomentellous ..... *P. glabrifolium*
34(30). Leaves clustered at tips of branches ..... 35
34. Leaves not clustered ..... 37
35(34). Leaves at base abruptly cordate, the tip acuminate; petioles to 8 mm long; inner surface of tepals papillose ..... *P. williamsii*
35. Leaves at base attenuate to cuneate, tip obtuse; petioles to 17 mm long; inner surface of tepals tomentellous ..... 36
36(35). Tepals spreading at anthesis, subequal; androecium not at top of a short, pubescent column; leaf base cuneate; lower leaf surface covered with very short, ± hairlike papillae ..... *P. crassitepalum*
36. Tepals reflexed at anthesis, equal; androecium situated on top of a short, pubescent column; leaf base obtuse or (on shade-leaves) acute; lower leaf surface glabrous or with few scattered, erect hairs, never with a cover of papillae ..... *P. tomiwahlii*
37(34). Inner surface of tepals pubescent; pistil glabrous ..... 38
37. Inner surface of tepals papillose; pistil papillose or pubescent (in *P. steyermarkianum* pistil glabrous) ..... 40
38(37). Marginal vein prominent on lower leaf surface ..... *P. marginale*
38. Marginal vein lacking on lower leaf surface 39
39(38). Lateral veins 15–20 on each side; flowers 15–17 mm diam., inner tepals narrower than outer ones ..... *P. grandiflorum*
39. Lateral veins 5–8 on each side; flowers 8 mm diam., tepals equal ..... *P. westphalii*
40(37). Leaf base abruptly rounded or abruptly cordate; petioles thick, to 8 mm long ..... 41
40. Leaf bases acute, obtuse or rounded, but never abruptly rounded; petioles 6–30 mm long (*P. nobile*, with rounded leaf bases, has petioles 20–30 mm long) ..... 42
41(40). Pedicels ca. 3 mm long; leaves narrowly obovate or oblanceolate; Amazonian Peru and Ecuador ..... *P. williamsii*
41. Pedicels 1.5–2 cm long; leaves obovate; Panama and Costa Rica . *P. hexaglandulosum*
42(40). Bracts of inflorescences present at anthesis; leaf tips sharply acute to acuminate; upper leaf surface dull ..... *P. golfodulcense*
42. Bracts of inflorescences lacking at anthesis; leaf tips obtuse to acute; upper leaf surface somewhat shiny ..... 43
43(42). Style densely gray-pubescent; receptacle pubescent inside ..... *P. cinereum*
43. Style glabrous or brown-papillose; receptacle glabrous inside ..... 44
44(43). Lateral veins 7–10 on each side; glands forming a flat, pillowlike mass ..... *P. nobile*
44. Lateral veins 11–16 on each side; glands forming ridges surrounding stamens ..... *P. steyermarkianum*

**Pleurothyrium acuminatum** van der Werff, sp. nov. TYPE: Peru. Loreto: Prov. Requena, Arboretum Jenaro Herrera, *van der Werff, Vasquez & Jaramillo 9967* (holotype, MO; isotypes, AAU, AMAZ, BR, C, F, G, HBG, K, MEXU, NY, QRS, S, U, US, USM). Figures 10, 11.

Arbor. Ramuli teretes, solidi, dense, minute adpresse pubescentes. Gemma terminalis dense, adpresse pubescens. Folia alterna, tenuiter chartacea, 10–20 × 3–6 cm, elliptica, basi sensim in petiolum attenuata, apice acuminata, acumine 1–1.5 cm longo, supra glabra, punctata, subtus glabra vel pilis minutis adpressis praedita praecipue secus costam nervosque et ad basim; nervis lateralibus 6–10 utroque costae latere, sursum arcuatis et in dimidio distali parum brochidodromis; venatione supra immersa, subtus costa elevata, nervis et venatione paullo elevata. Petioli 1  2 cm longi, supra applanati, basi paullo incrassati. Inflorescentiae ex axillis cataphyllorum ortae, 8–12 cm longae, graciles, ramulis semel vel bis de modo cymae furcatis, tomentellae, bracteis deciduis. Pedicelli (4–)5(–8) mm longi, tomentelli. Flores albi. Tepala 6, aequalia, per anthesin plerumque erecta, oblonga, 3 × 1 mm, saepe torta, sed marginibus non reflexis, tres exteriora extus minute puberula vel papillosa, tres interiora extus basi papillosa, demum glabra, omnia intus parum papillosa vel glabra. Receptaculum ad apicem constrictum. Stamina 9, 4-locellata, locellis lateralibus et sursum aperientibus. Filamentis antheris aequantibus; glandulis incrassatis, liberis. Pistillum ca. 1.5 mm longum, ovario ellipsoideo, 1 mm longo, dimidio basale glabro, dimidio distale parum pubescente, stylo pubescente. Fructus ignoti.

FIGURE 10. *P. acuminatum.*—A. Habit.—B. Flower showing abscission line of tepals.—C. Floral detail.—D. Young fruit.—E. Stamens—Whorl I on right, Whorl II in center, Whorl III on left.—F. Branching pattern of inflorescence.

Tree, 15 m. Twigs terete, solid, densely, but minutely appressed gray pubescent, 3 mm diam. ca. 5 cm below the tip. Terminal bud somewhat shiny, densely appressed-pubescent. Leaves alternate, thinly chartaceous, 10–20 × 3–6 cm, elliptic, the base gradually narrowed in the petiole, the tip acuminate, the acumen 1–1.5 cm long, the upper surface glabrous and gland-dotted, this best visible on young leaves, the lower surface glabrous or with some minute appressed hairs, especially along the veins and near the base; lateral veins 6–10 on each side, arching upward near the margin and weakly loop-connected in the upper half of the lamina; venation immersed on upper surface, midrib raised on lower surface, the lateral veins and tertiary venation less so. Petioles 1–2 cm long, adaxially flattened, somewhat swollen near the base, with a similar indument as the twigs. Inflorescences

FIGURE 11. Distribution of *P. acuminatum* (★), *P. amapaense* (●), *P. amplifolium* (○), and *P. bifidum* (■).

in axils of cataphylls, 8–12 cm long, slender, laxly branched, the branchlets once or twice cymosely branched, minutely tomentose, bracts deciduous at anthesis. Pedicels (4–)5(–8) mm long, minutely tomentellous. Flowers white. Tepals 6, equal, mostly erect at anthesis, oblong, 3 × 1 mm, often wrinkled, twisted, but the margins not consistently inrolled, the outer 3 minutely puberulous to papillose outside, the inner 3 with a papillose, triangular base, otherwise glabrous, the inside slightly papillose to glabrous. Tepals united at the very base and falling from old flowers as a unit. Receptacle constricted at the tip, the constriction line turning into a dehiscence line in older flowers. Stamens 9, 4-celled, the cells lateral and opening upward, filaments about as long as anthers, glabrous; glands enlarged, protruding between the outer stamens, free. Pistil ca. 1.5 mm long, ovary 1 mm long, the lower half glabrous, the upper half slightly pubescent, style pubescent. Receptacle glabrous inside. Fruit unknown. Flowers: August–September. Elevation range: 100–200 m.

*Collections studied.* BRAZIL. AMAZONAS: São Paulo de Olivenca, *Ducke RB25676* (RB). PERU. LORETO: Requena, Arboretum of Jenaro Herrera, *?* (MO), *? s.n.* (MO), *Castillo 50* (F, MO), *van der Werff 9967* (AAU, AMAZ, BR, C, F, G, HBG, K, MEXU, MO, NY, QRS, S, U, US, USM).

*Pleurothyrium acuminatum* is only known from a few collections from the Arboretum Jenaro Herrera in Amazonian Peru and one collection from Amazonian Brazil. It is included and illustrated in Spichiger et al. (1989) as *Ocotea undulata* (Meissner) Mez, a species that I place in *Pleurothyrium* and which is closely related to *P. acuminatum*. The erect tepals at anthesis, the relatively small (for *Pleurothyrium*) glands, the shape of the pistil and tepals, and the weakly loop-connected lateral veins all point to the group of species with reflexed margins of tepals as the closest relatives of *P. acuminatum*, even though the margins of the tepals are plane in this species. The other main group of *Pleurothyrium*, characterized among others by rotate flowers, has much broader tepals and usually

larger, fused glands. Within the group of *Pleurothyrium* species with erect tepals, *P. acuminatum* stands apart by its rather long tepals with a plane margin, long, slender pedicels, and the very short, almost papillose indument of the flowers. The acuminate leaves are also a useful character.

**Pleurothyrium amapaense** Allen, Mem. New York Bot. Gard. 15: 92. 1966. TYPE: Brazil. Amapá: Rio Araguari, *Pires et al. 51430* (holotype, NY not seen; isotypes, K, S, US). Figure 11.

Tree, 15 m tall. Twigs terete, solid, the young parts ferruginous-tomentellous, older parts glabrous and with pale bark. Terminal bud ferruginous-tomentellous. Leaves clustered at the tips of branches, chartaceous, elliptic-obovate to elliptic, 10–20 × 4–6 cm, the base cuneate, the tip shortly acuminate, glabrous, lateral veins 8–10 on each side, curving upward near the margin and loop-connected in the upper half of the lamina; venation immersed on upper surface, costa and lateral veins raised on lower surface. Petioles ca. 1 cm long, narrowly canaliculate, with similar indument as twigs. Inflorescences in axils of deciduous bracts, ferruginous-tomentellous, to 12 cm long, paniculate, the branches once or twice cymosely branched, bracts lacking at anthesis. Pedicels slender, 4–5 mm long, ferruginous-tomentellous. Flowers greenish brown fide collectors, ca. 5 mm diam. Tepals 6, equal, minutely tomentellous outside, papillose inside, ovate, 2–2.5 mm long, often twisted, spreading or reflexed in old flowers, finally breaking off along a dehiscence line at the base, the margin plane. Stamens 9, 4-celled, the cells lateral, opening upward, anthers glabrous, filaments about as long as anthers; glands enlarged, free, falling off in old flowers. Pistil ca. 2 mm long, ovary ellipsoid, glabrous near base, becoming progressively more papillose toward the tip, style densely papillose, 0.5 mm long, stigma small. Floral tube deeper than wide, glabrous inside. Fruits unknown. Flowers: October. Elevation range: ca. 100 m.

*Collections studied.* BRAZIL. AMAPA: Rio Araguari, *Pires 51430* (K, NY, S, US). VENEZUELA. AMAZONAS: Río Negro, upper Río Baria, *Davidse 27524* (MO, VEN).

*Pleurothyrium amapaense* is the only *Pleurothyrium* species reported east of Manaus, Brazil. It is only known from the type collections, but as Allen (1966a) already stated, there can be no doubt about its generic position. *Pleurothyrium amapaense* has, for the genus, rather small flowers; it differs from the other small-flowered species in having tepals with plane, not reflexed, margins, in having clustered leaves, and in its ferruginous indument.

Provisionally included here is *Davidse 27524* (MO), collected from Depto. Río Negro, Territorio Federal Amazonas, Venezuela. This collection differs in its thinner leaves, shorter pubescence, more elliptic leaves with a less well-developed marginal vein, and its habit (label states it is a liana). The floral characteristics agree reasonably well with those of *Pleurothyrium amapaense*, but it is possible that, once more collections are at hand, it is better recognized as a distinct species.

**Pleurothyrium amplifolium** (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra amplifolia* Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 131. 1892. TYPE: Brazil. Rio de Janeiro: Alto Macahé, *Glaziou 17731* (holotype, B; isotypes, B, G, K, NY, P). Figure 11.

Tree, size unknown. Twigs terete, solid, brown-tomentellous, glabrescent, ca. 4 mm diam. 5 cm below apex. Terminal bud brown-tomentellous. Leaves alternate, chartaceous, elliptic to broadly elliptic, 15–20 × 7–10 cm, the base obtuse or slightly acute, the apex rounded or shortly acute, upper surface glabrous and with venation immersed, the lower surface minutely puberulous when young, soon glabrescent, costa and lateral veins raised, tertiary venation immersed; lateral veins 8–11, arching upward near the margin, not loop-connected. Petioles 8–14 mm long, the upper side flat, with similar pubescence as twigs. Inflorescences in axils of cataphylls, brown-tomentellous, 8–12 cm long, paniculate, the branchlets 1–2 times cymosely branched, flowers more than 30, bracts absent at anthesis. Flowers ca. 4 mm diam. Tepals 6, equal, ± erect at anthesis, the margin reflexed, brown-tomentellous outside, but inner three tepals with papillose margin and tip, all tepals papillose inside. Stamens 9, 4-celled, glabrous, the outer six with one pair of cells lateral and one pair introrse, the inner three with one pair extrose and one pair lateral; filaments clearly visible between glands, ca. 0.5 mm long, longer than anthers; glands enlarged, visible as triangular lobes between the outer stamens, but very low in front of the stamens and not fused. Pistil ellipsoid, ca. 1.5 mm long, ovary glabrous, style papillose. Receptacle glabrous except for a few hairs at the very base. Fruit and cupule unknown. Flowers: October. Elevation range unknown.

*Collection studied.* BRAZIL. RIO DE JANEIRO: Alto Macahe, *Glaziou 17731* (B, G, K, NY, P).

*Pleurothyrium amplifolium* is only known from the type and is also, if the label data are correct, the only *Pleurothyrium* species from southern Brazil. It belongs in the group of species with reflexed margins of tepals, small flowers, often with erect tepals and a poorly developed (or without a) marginal vein. It stands apart from the other species in this group by its distribution, broad leaves, and indumentum.

Three isotypes were annotated as *Persea cordata* Mez var. *glabra* Mez, but the holotype does not bear this annotation. *Persea cordata* var. *glabra* is a numen nudum included in Glaziou's list of determinations, while *Persea cordata* (Vell.) Mez, the correct citation, is a later homonym of *Persea cordata* Meissner.

**Pleurothyrium bifidum** Nees, Syst. Laur.: 351. 1836. TYPE: Peru. Loreto: Yurimaguas, *Poeppig 2398* (GZU, LE, W destroyed?, holotype not designated). Figure 11.

Tree, to 10 m. Twigs terete, glabrous or nearly so, solid. Terminal bud brown-tomentulose. Leaves alternate, said to be clustered near tips of branches, subcoriaceous, elliptic to obovate-elliptic, 30–40 × 8–13 cm, the base obtuse or acute, the tip acuminate, acumen to 3 cm long, the upper surface glabrous, lower surface covered with a dense, minute, gray-whitish tomentellous indument; venation immersed on upper surface, midrib and lateral veins raised on lower surface, tertiary venation not visible; lateral veins 12–16 on each side, weakly loop-connected in the distal half of leaf. Petioles 3–5 cm long, glabrous. Inflorescences in axils of cataphylls, ferruginous-tomentellous, 15–25 cm long, paniculate, the upper branchlets once or twice cymosely branched, the lower ones racemosely branched, but ultimate divisions cymose; bracts subpersistent at anthesis; brown-tomentellous outside, glabrous inside. Flowers white or creamy-white, 10–12 mm diam. Tepals 6, the inner three with a slightly narrower base than the outer ones, broadly elliptic, 4–5 mm long, the outer three ferruginous-tomentellous outside, the inner three with a tomentellous, triangular basal patch, otherwise papillose; inside papillose. Stamens 9, 4-celled, the cells lateral or one pair lateral-extrorse, the valves back-to-back, glands large, completely surrounding stamens, but not fully fused. Ovary ellipsoid, ca. 1 mm long, densely papillose, with 6 glabrous patches near the tip, style short, ca. 0.5 mm long, glabrous, stigma platelike. Floral tube papillose inside. Cupule a rather shallow cup, ca. 2 cm wide and 1 cm high, verrucose, the pedicel swollen; fruit ellipsoid, 2.5 × 1.5 cm. Fruits: September. Flowers: June–September. Elevation range: 200–500 m.

*Collections studied.* PERU. AMAZONAS: Río Cenepa, Quebrada Chigka Entsa, *Ancuash 602* (G, MO); Bagua, Cascadas de Mayasi, along Quebrada Tambillo, *Wurdack 2047* (F, GH, K, NY, S, US). LORETO: Yurimaguas, *Poeppig 2398* (GZU, LE).

*Pleurothyrium bifidum* is an uncommon species, only known from three collections in Amazonian Peru. The type specimens (GZU, LE) are in bud, thus I have not been able to study flowers of the type. A type photograph (A) of the type in W shows that this specimen, probably destroyed in World War II, was also largely in bud. My floral description is based on the two recent collections and agrees with earlier floral descriptions based on the type collection. Nees stated in the original description that the leaves were clustered, but the type specimens at hand have a very short piece of the twig, which does not show if the leaves were clustered or not; the W type had clustered leaves, as can be seen on the type photo. The recent collections have the leaves more or less clustered. However, the recent material differs from the types in having thicker twigs and narrower leaves; in other characters it agrees with the type.

*Pleurothyrium bifidum* is closely related to *P. panurense* (Meissner) Mez, as is shown by the, for *Pleurothyrium*, very unusual, whitish indument on the lower leaf surface. *Pleurothyrium bifidum* has larger leaves and longer inflorescences and petioles than *P. panurense*; it also has a papillose ovary and floral tube (glabrous in *P. panurense*), and the flowers are slightly larger and have the inner surface of the tepals brown-papillose (glabrous in *P. panurense*). The size differences do not allow easy identification. For instance, *Krukoff 4800* is identified as *P. panurense* based on floral characters; its leaves can be interpreted equally well as large *P. panurense* or small *P. bifidum*.

Kostermans (1952) made combinations for a number of *Pleurothyrium* species in *Ocotea*; he accepted for *Pleurothyrium bifidum* the name *Ocotea bifidum* Poeppig ex Nees. However, *Ocotea bifidum* is a herbarium name cited by Nees as a synonym in the description of *P. bifidum* and is, therefore, not validly published.

**Pleurothyrium bracteatum** van der Werff, sp. nov. TYPE: Colombia. Boyaca: El Humbo, ca. 130 mi. N of Bogotá, elev. 3,000 ft., *Lawrance 619* (holotype, MO; isotypes, E, F, UC, US). Figures 12, 13.

FIGURE 12. *P. bracteatum.*—A. Habit.—B. Detail of inflorescence showing bracts and flower.—C. Cross section through flower, showing pistil and stamens embedded in glands.—D. Pistil.—E, F. Stamens.—G. Detail of upper leaf surface.—H. Detail of lower leaf surface.

Arbor, 20–25 m alta. Ramuli solidi, teretes vel paullo angulati, rufo-tomentosi. Gemma terminalis ad 7 mm crassa, rufo-tomentosa. Folia alterna, subcoriacea, 15–30 × 8–12 cm, oblonga vel oblongo-elliptica, basi rotundata, apice paullo acuta, supra glabra, subtus rufo-tomentosa, nervis lateralibus 14–20 utroque costae latere, prope marginem sursum curvantibus, vena marginale in dimidio distale praesente, venatione supra immersa, subtus costa nervisque lateralibus elevatis, venatione tertia paullo elevata. Petioli rufo-tomentosi, valde canaliculati, 10–15 mm longi. Inflorescentiae ex axillis bractearum ortae, rufo-tomentosae, 10–15 cm longae, paniculatae, ramulis vulgo duplo cymae more ramosis; bracteis sub anthesi praesentibus, rufo-tomentosis, eis ad ramulorum inferiorum basim ovatis, 12–15 mm longis, eis ad cymarum terminalium basim ca. 5 mm longis. Pedicelli florum apertorum ca. 8 mm longi. Flores cremei, saltem 13 mm diametro. Tepala 6, subaequalia, late ovata, ca. 5 mm longa, intus tomentella. Stamina 9, glabra, 4-locellata, locellis lateralibus, glandulis permagnis, coalitis, stamina cingentibus. Ovarium ellipsoideum, ca. 1.3 mm longum, basi glabrum, parte media tomentellum, parte superiore tomentellum 6 maculis nudis praeditum; stylum glabrum, ca. 1 mm longum. Tubus floralis intus tomentellus. Fructus ignotus.

Tree, 20–25 m tall. Twigs solid, terete or slightly ridged, reddish-brown-tomentose, 5–6 mm diam. 5 cm below the tip. Terminal buds to 7 mm thick, rufous-tomentose. Leaves alternate, subcoriaceous, 15–30 × 8–12 cm, oblong to oblong-elliptic, the base rounded, the tip slightly acute, glabrous above, rufous-tomentose below, venation immersed on upper surface, midrib and lateral veins raised on lower surface, the tertiary venation slightly raised; lateral veins 14–20 on each side, curving upward near the margin and united with the superior vein, forming a marginal vein in the upper half of the lamina.

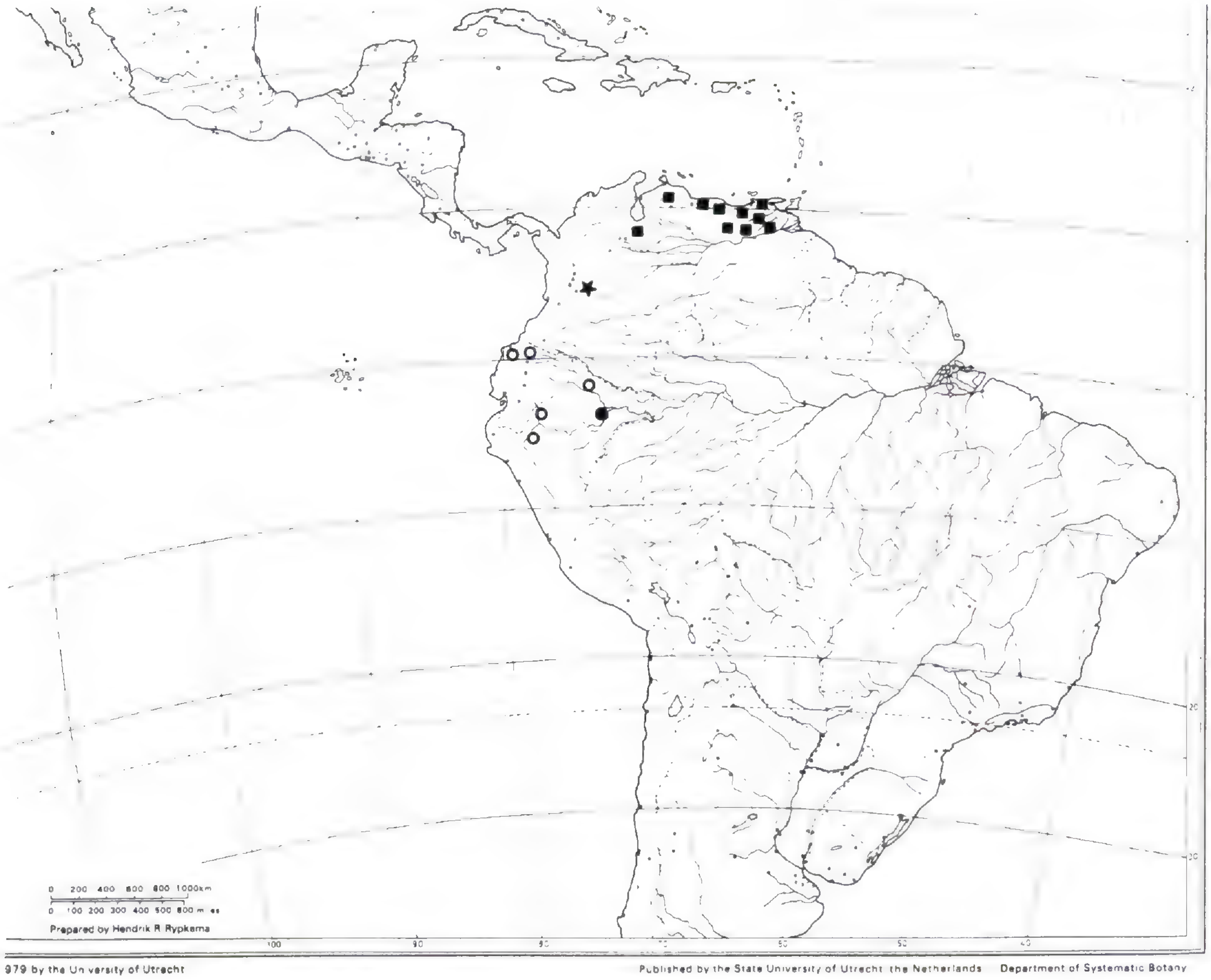



FIGURE 13. Distribution of *P. bracteatum* (★), *P. brochidodromum* (●), *P. cinereum* (○), and *P. costanense* (■).

Petioles rufous-tomentose, strongly canaliculate, 10–15 mm long. Inflorescences in axils of cataphylls, rufous-tomentose, 10–15 cm long, paniculate, the branchlets usually twice cymosely branched; bracts present at anthesis, those at the base of the lower branchlets 12–15 mm long, ovate, rufous-tomentose, gradually reduced in size toward the ultimate divisions, the bracts at the base of the ultimate cymes ca. 5 mm long. Pedicels of open flowers ca. 8 mm long, rufous-tomentose. Flowers creamy white inside, at least 13 mm diam. (none of the flowers had all tepals spreading). Tepals 6, ± equal, broadly ovate, ca. 5 mm long, the outer three tomentose on the outside, the inner three with a tomentose, basal triangular patch, otherwise tomentellous; all tepals tomentellous inside. Stamens 9, glabrous, 4-celled, the cells lateral and opening back-to-back, the glands strongly enlarged and forming a thick wall surrounding the stamens, fused. Ovary ellipsoid, ca. 1.3 mm long, the very base glabrous, the middle part brown-tomentellous, the upper part tomentellous with 6 bare spots where glands touched the ovary; style ca. 1 mm long, glabrous. Floral tube rather deep, brown-tomentellous inside. Fruit unknown. Flowers: February. Elevation range: ca. 1,000 m.

*Collection studied.* COLOMBIA. BOYACA: El Humbo, *Lawrance 619* (E, F, MO, UC, US).

*Pleurothyrium bracteatum* is only known from the type collection from the El Humbo region in Boyaca, Colombia; this area also yielded *Aiouea angulata* Kostermans, another Lauraceae only known from the type collected by Lawrance.

This new species can be readily identified by the large bracts of the inflorescence, which persist during anthesis. Other useful characters are the rufous pubescence (described by the collector as burnt sienna), the rounded leaf bases, and large flowers. It can be confused with *Pleurothyrium costanense* from similar elevation in Venezuela, but the latter species lacks bracts at anthesis, has smaller flowers, a distinctly pubescent style, and an almost glabrous ovary.

The collector noted that the stamens were in the form of a button. The wood is said to be soft and has no economic uses.

**Pleurothyrium brochidodromum** van der Werff, sp. nov. TYPE: Peru. Loreto: Maynas, km 32 of Carretera Iquitos–Nauta, *Vasquez & Jaramillo 7865* (holotype, MO; isotypes, AMAZ, F, G, HBG, NY, USM). Figures 13, 14.

Arbor, 16 m alta. Ramuli teretes, solidi, ferrugineo-tomentosi, glabrescentes. Gemma terminalis fusco-tomentosa, magna, ad 5 mm diametro. Folia ad ramulorum apices conferta, chartacea, 12–22 × 4–7 cm, elliptica vel obovato-elliptica, basi acuta, apice acuminata, supra glabra sed costa pilis parvis praedita, subtus pilis dispersis, erectis praedita (secus costam nervosque indumento densiore); supra venatione immersa, subtus costa nervisque elevata, venatione tertia paullo elevata; nervis utroque costae latere 12–15 in vena maginale terminantibus. Petioli 1.5–2 cm longi; teretes, indumento illo ramuli simile. Inflorescentiae ex axillis bractearum ortae, 8–14 cm longae, ferrugineo-tomentosae, paniculatae, ramulis 1–2-plo cymae more divisis. Flores 9–10 mm diametro. Tepala 6, aequalia, 3–4 mm longa, oblonga, intus ferrugineo-papillosa, extus ferrugineo-tomentella (tepala interiora margine et apice papillosa). Stamina 9, 4-locellata, locellis lateralibus, minute papillosa; glandulae magnae, stamina cingentes, coalitae. Ovarium parvum, ovoideum, in stylum attenuatum, stigmate antheris obtecto. Fructus ignotus.

Tree, 16 m tall. Twigs terete, solid, ferruginous-tomentose, but soon glabrescent, 3–4 mm diam. 5 cm below tip. Terminal bud large, 5 mm thick, fuscous tomentose. Leaves clustered near tips of branches, chartaceous, 12–22 × 4–7 cm, elliptic to obovate-elliptic, the base acute, the tip acuminate, the upper surface glabrous except for some short hairs on midrib, the lower surface with scattered, brown, erect hairs, these denser along main veins and midrib; venation immersed on upper surface, midrib, lateral veins, and to a lesser degree tertiary venation raised on lower surface; lateral veins 12–15 on each side, the lower 2–3 arching upward, the other ones ± straight and ending in a well-developed marginal vein. Petioles 1.5–2 cm long, terete, with similar indument as twig, ca. 2 mm diam. Inflorescences in axils of cataphylls, 8–14 cm long, ferruginous-tomentose, paniculate, the branchlets 1–2 times cymosely branched, ca. 40-flowered, bracts often persisting at anthesis, ferruginous-tomentose on both surfaces, to 4 mm long (but bracts subtending flowers smaller), elliptic. Flowers green fide collectors, 9–10 mm diam. Tepals 6, equal, 3–4 mm long, oblong, spreading to slightly reflexed at anthesis, the inner surface ferruginous papillose, the outer tepals ferruginous-tomentellous on the outside, the inner three with papillose margin and tip, otherwise tomentellous. Stamens 9, all 4-celled, finely papillose, the cells lateral; stamens ca. 1 mm long, the filaments short and nearly as wide as the anthers; glands conspicuously enlarged, completely surrounding the stamens, fused. Ovary small, ovoid, the very base glabrous, situated in the glabrous, shallow receptacle, with a band of coarse papillae near the middle, the upper part gradually narrowed into the style, finely papillose, pistil ca. 1.4 mm long; stigma in all flowers seen not exposed, but covered by the anthers. Floral tube glabrous. Fruits unknown. Flowers: August. Elevation range: ca. 150 m.

*Collection studied.* PERU. LORETO: Maynas, Carretera Iquitos–Nauta, km 32, *Vásquez 7865* (AMAZ, F, G, HBG, MO, NY, USM).

*Pleurothyrium brochidodromum*, only known from the type collection made near Iquitos, Peru, is easily identified by its sparse, erect pubescence on the lower leaf surface, clustered leaves, and floral size. Other *Pleurothyrium* species from Amazonian Peru with an erect pubescence on lower leaf surface include *P. insigne* and *P. vasquezii*. *Pleurothyrium insigne* differs in its much larger, obovate leaves, while *P. vasquezii* differs in its alternate (not clustered) leaves and smaller flowers (5–6 mm vs. 9–10 mm in *P. brochidodromum*).

A brochidodromous venation type is relatively common in *Pleurothyrium*, but is particularly clearly visible in *P. brochidodromum*. However, in such species as *P. maximum* and *P. williamsii* the brochidodromous venation is equally well developed.

Although the type collection has good young and old flowers, the stigma is hidden in all flowers seen. This is unusual in *Pleurothyrium*; normally in the species with large flowers and greatly enlarged glands the stigma is large, almost platelike, and easily visible.

**Pleurothyrium cinereum** van der Werff, sp. nov. TYPE: Ecuador. Esmeraldas: Panadero, 5 km from the river, *Játiva & Epling 2039* (holotype, MO; isotypes, NY, US). Figures 13, 15.

Arbor ad 32 m. Ramuli angulares, fusco-tomentelli, glabrescentes, solidi. Folia alterna, firme chartacea, 13–20 × 6–10 cm, elliptica, basi obtusa, apica acuta, raro obtusa, supra venatione impressa, subtus costa nervisque (10–14 utroque costae latere) elevatis, reticulatione paullo elevata, venatione in dimidio distale brochidodroma, supra glabra, subtus pilis parvis adpressis praedita. Petioli canaliculati, 1.5–2.5 cm longi. Inflorescentiae e axillis cataphyllorum ortae, fusco-tomentellae, 10–15 cm longi, ramulis semel vel bis cymae more divisis. Pedicelli ca. 5

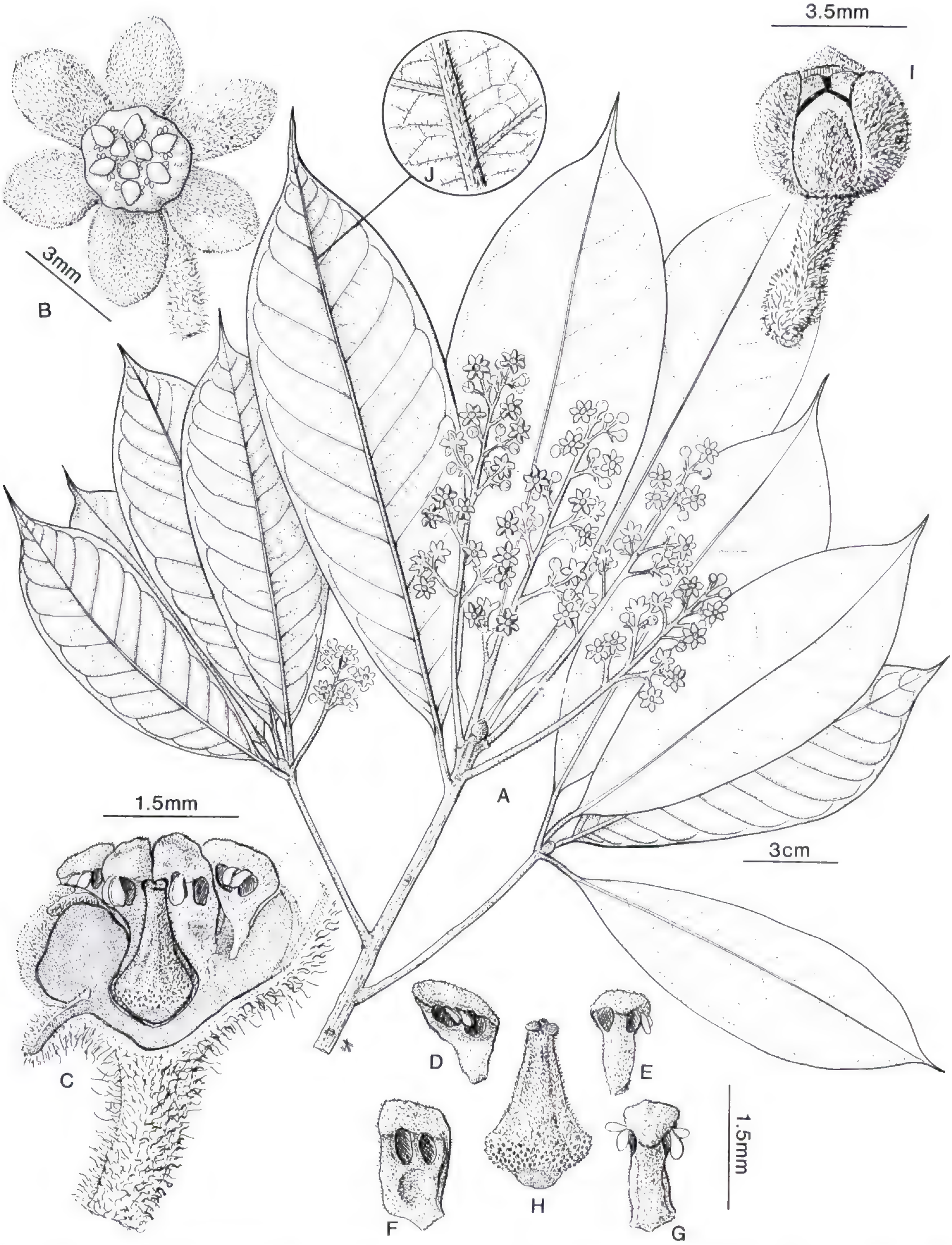



FIGURE 14. *P. brochidodromum.* —A. Habit.—B. Flower.—C. Cross section through flower.—D, E. Lateral and frontal views of outer stamen.—F, G. Lateral and frontal views of inner stamen.—H. Pistil.—I. Bud, showing indument on inner and outer tepals.—J. Detail of lower leaf surface.

mm longi. Flores rotati, 11 mm in diametro. Tepala 6, subaequalia, 3 exteriora late elliptica vel rotundata, 4 × 4 mm, extus cinereo-pubescentia, 3 interiora elliptica, 4 × 3 mm, secus basim angustata, extus cinereo-puberuli sed basi cinereo-pubescenti, omnia intus papillosa basi cinero-pubescenti. Stamina 9, 4-locellata, locellis dorsali-lateralibus; glandulis perdilatatis, fere stamina cingentibus, connatis. Pistillum ad 2 mm longum, cinereo-pubescens,

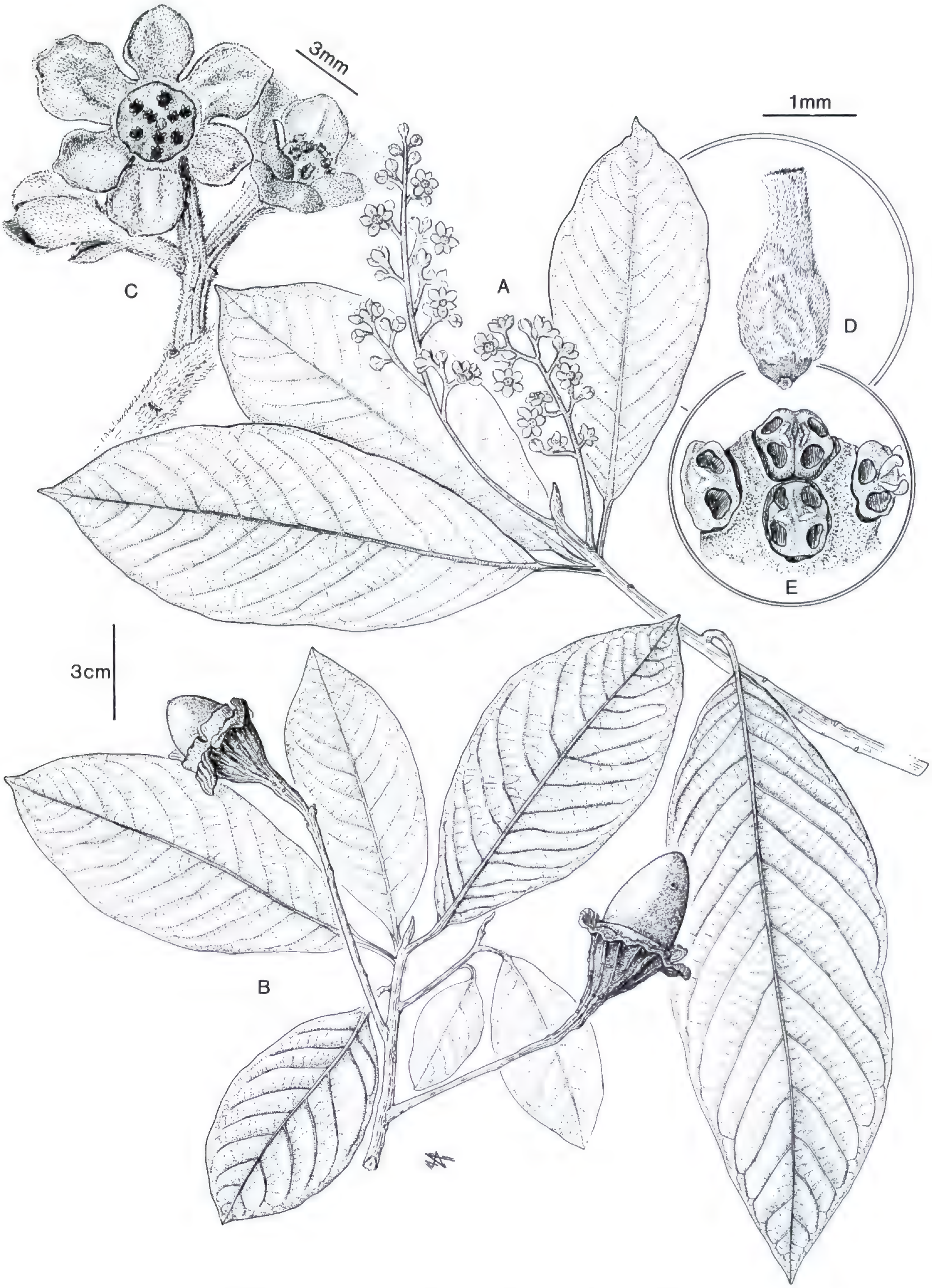



FIGURE 15. *P. cinereum*.—A. Habit, flowering.—B. Habit, fruiting.—C. Flower.—D. Pistil.—E. Detail of flower, showing embedded anthers. B from *Gentry & Smith 45117*, others from *Neill 8954*.

ovario ellipsoideo, sensim in stylum attenuato. Receptaculum intus cinereo-pubescens. Cupula profunda, lenticellata, tepalis persistentibus. Fructus ellipsoideus, ad 6 cm longus.

Tree, to 32 m tall, with buttresses. Twigs angular, brown-tomentellous, becoming glabrous with age, solid, 4 mm diam. ca. 5 cm below apex. Terminal bud brown-tomentellous, about as wide as the twig. Leaves alternate, firmly chartaceous, 13–20 × 6–10 cm, elliptic, the base obtuse, the tip acute, rarely obtuse, venation impressed on upper surface, midrib and lateral veins (10–14 on each side) raised on lower surface, tertiary venation slightly raised, lateral veins weakly loop-connected in the distal half of lamina, upper surface glabrous, the lower surface with varying amounts of minute, appressed hairs. Petioles canaliculate, 1.5–2.5 cm long, with similar indument as twigs. Inflorescences in axils of cataphylls, brown-tomentellous, 10–15 cm long, the branchlets once or twice cymosely branched, bracts deciduous at anthesis. Pedicels ca. 5 mm long. Flowers rotate, 11 mm diam. described as creamy-white, yellowish-ferruginous or brick-red. Tepals 6, subequal, the outer three broadly ovate to rounded, 4 × 4 mm, gray-pubescent outside, the inner three elliptic, 4 × 3 mm, narrowed toward the base, gray-puberulent outside except for a basal, triangular, gray-pubescent patch; all tepals papillose inside except for the gray-pubescent base. Stamens 9, all 4-celled, the cells dorsal-lateral and opening back-to-back; glands strongly enlarged, almost completely surrounding the outer stamens, fused. Pistil ca. 2 mm long, gray-pubescent, ovary ellipsoid and gradually narrowed into the style, the gray-pubescent style in dried flowers visible above the androecium. Floral tube gray-pubescent inside. Cupule deeply cup-shaped, lenticellate, 2 × 2.5 cm, tepals persisting on the margin of the cupule. Fruit an ellipsoid berry, to 6 cm long. Fruits: February–May. Flowers: May, July. Elevation range: sea level to 1,600 m.

*Collections studied.* ECUADOR. ESMERALDAS: Río Onzole, *Jativa 1104* (NY); Panadero, N of San Lorenzo, *Janse 280* (MO, NY, US); Panadero, 5 km from river, *Jativa 2039* (MO, NY, US); Panadero, *Little 21359* (MO, QAME). NAPO: Archidona, S slopes of Volcán Sumaco, *Neill 8954* (MO). PERU: LORETO: Florida, mouth of Río Zubineta in Río Putumayo, *Klug 2122* (A, F, G, GH, K, MO, S, US); Pongo de Manseriche, mouth of Río Santiago in Marañon, *Tessmann 4634* (G). SAN MARTIN: *A. Gentry & D. N. Smith 45117* (MO).

*Pleurothyrium cinereum* is known from several rather widely separated localities. The type collection is from the coast near Esmeraldas, Ecuador. *Little et al. 21359* was collected the same day at the same locality and likely came from the same tree. *Janse 280*, a fruiting collection, is also from Esmeraldas. *Neill et al. 8954* was collected on the slopes of volcano Sumaco 1,150 m elevation, Napo province, Ecuador. This collection, with flowers and a fruit, has slightly smaller and more pubescent leaves than the Esmeraldas specimens and has the pleasant odor commonly encountered in *Aniba*. The third locality is along the Río Putumayo, Dept. Loreto, Peru, at 180 m elevation. The specimens from Esmeraldas have creamy-white flowers, from volcano Sumaco yellowish-ferruginous, and from Peru brick-red flowers. The collections all possess a slightly shiny upper leaf surface, a pubescent style, very slight difference in pubescence on outer surface of tepals between inner and outer tepals (much less than common in the genus), and frequently an obtuse leaf base. Visibly pubescent styles are very uncommon in *Pleurothyrium* and are an important reason for placing these collections in one species. *Pleurothyrium cinereum* is included in Little & Dixon (1969) as *Pleurothyrium* sp.

Vegetatively *P. cinereum* strongly resembles *P. steyermarkianum*. The latter species has quite different flowers (with glands forming ridges, not a central dome, and a glabrous style), and its pedicels are strongly triangular in cross section.

The common name used by the Huitot Indians, cited by Klug, is Naime-ey.

The epithet *cinereum* refers to the gray-pubescent style, one of the most distinctive features of this species.

Provisionally placed here is a fruiting collection from the San Martin Province, 20 km NW from Rioja, elevation 1,000 m (*Gentry & Smith 45117*, MO). This collection has the denser indument also found in the Neill collection from Ecuador. In leaf characters it is a good match for *P. cinereum*. The fruit is large (4 × 2–2.5 cm) and the cupule has a double margin. The outer margin is formed by the persistent tepals and the inner margin is erect, ca. 0.5 cm taller than the outer one. Such a pronounced double margin has not been seen in other collections of *Pleurothyrium*. Remnants of stamens found on the cupule clearly point to *Pleurothyrium*; they have four lateral anther cells. The Neill collection includes one weakly double-margined cupule; cupules from Esmeraldas are less mature and do not show a double margin. If the Gentry collection is not an aberration, *P. cinereum* is the only *Pleurothyrium* species with a double-rimmed cupule.

**Pleurothyrium costanense** van der Werff, Ann. Missouri Bot. Gard. 74: 408. 1987. TYPE:

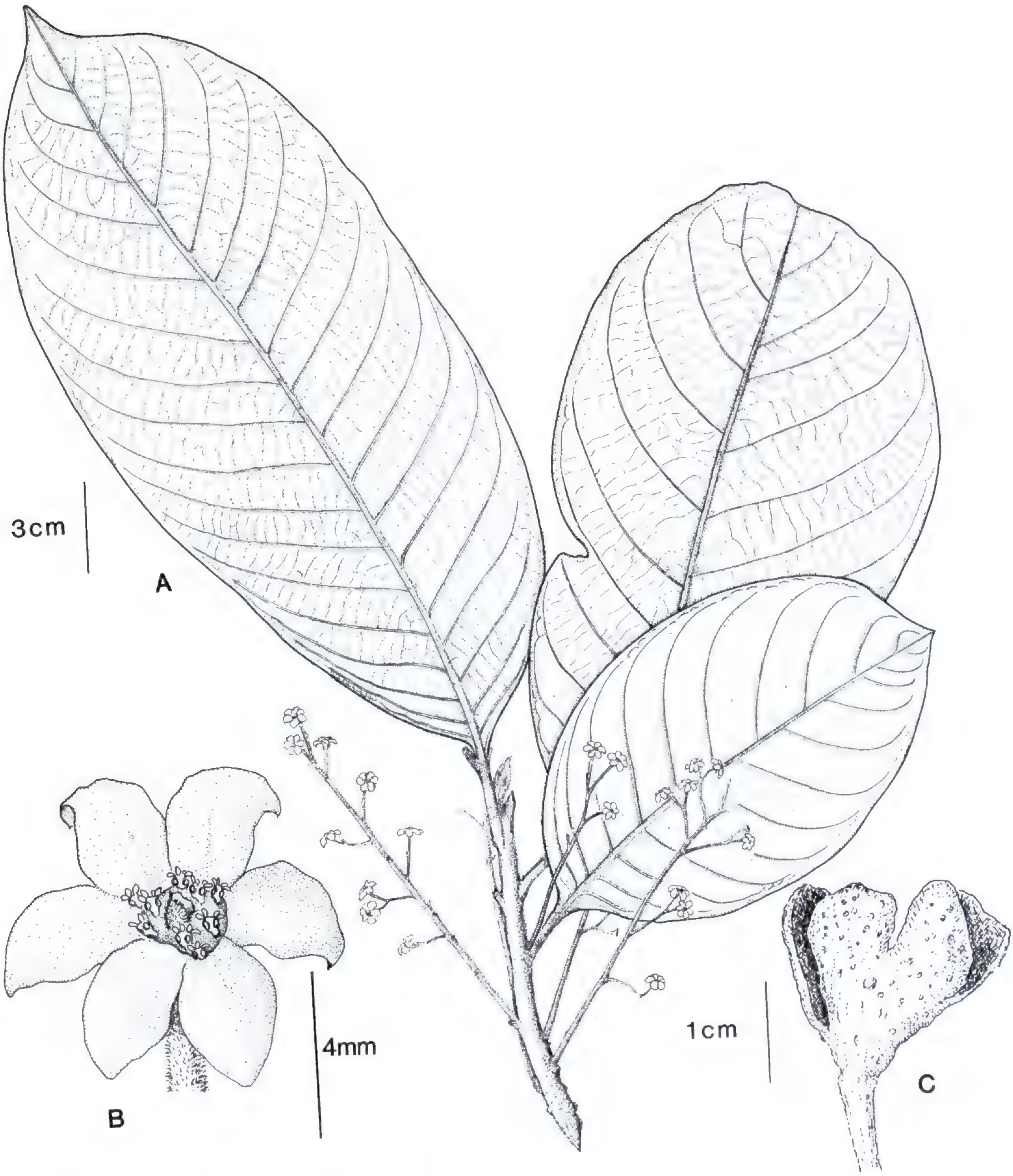



FIGURE 16. *P. costanense.*—A. Habit.—B. Flower.—C. Cupule.

Venzuela. Falcón: Sierra de San Luis, above La Chapa, *van der Werff 3654* (holotype, U; isotype, CORO). Figures 13, 16.

Tree, to 20 m tall. Twigs somewhat angular, ferruginous tomentose, but glabrescent with age, ca. 6 mm diam. 5 cm below apex, solid. Terminal bud ferruginous tomentose. Leaves alternate, chartaceous, 20–35 × 8–17 cm, elliptic to broadly elliptic, the base obtuse or acute, the apex rounded to shortly acuminate; upper surface with variable amounts of tomentose pubescence on midrib and lateral veins, othewise glabrous; lower surface with a ± dense cover of erect, ferruginous hairs, this becoming tomentose on midrib and lateral veins. Venation immersed on lower surface, but midrib, lateral veins, and tertiary venation raised on lower surface; lateral veins 10–17 on each side, arching near the margin toward the tip and becoming loop-connected in the distal half of the lamina. Petioles

1.7–3 cm long, ferruginous tomentose. Inflorescences in the axils of foliage leaves or cataphylls, ferruginous tomentose, 10–20 cm long, the branchlets 2–3 times cymosely branched. Flowers white or buff, 6–9 mm diam. Tepals 6, equal, spreading at anthesis, the outer 3 ferruginous pubescent outside, inner 3 puberulous outside except for a basal, triangular pubescent patch; all tepals papillose inside, elliptic, to 4 mm long. Stamens 9, all 4-celled, the outer 6 with the lower pair lateral-extrorse, the upper pair lateral-introrse, the inner 3 with extrorse or extrorse-lateral (upper pair) cells; filaments short, glabrous. Glands conspicuous, partly enclosing the outer stamens, but not fused. Ovary ellipsoid, with 6 longitudinal lines of hairs, otherwise glabrous, gradually narrowed in the conspicuously pubescent style; pistil ca. 2.8 mm long. Receptacle glabrous inside. Cupule large, warty. Fruits: March–August. Flowers: July–September. Elevation range: 700–2,200 m.

*Collections studied.* VENEZUELA. *Bernardi 6879* (G, MER, NY). ANZOATEGUI: Cerro Peonia, NE of Bergantin, *Steyermark 61393* (F). DISTRITO FEDERAL: mountain slope above Puerto Cruz, *Whitford 49* (A). FALCON: Sierra de San Luis, above la Chapa, *van der Werff 3654* (CORO, U). MERIDA: Andres Bello, La Carbonera, *Marcano Berti 1123* (MER, MO); Andres Bello, San Eusebio, *Quintero 11* (MER). MIRANDA: Paez, Fila La Tigra, 18 km SO de Cupira, *González & Ortega 1215* (G, MO). MONAGAS: Pueblo de Yucucual, *Lau 10* (MO); Montaña de Aguacate, *Steyermark 62230* (F); Caripe, Juasjuillar, *Bosque J-03* (MO), *Bosque J-03A* (MO), *Bosque J-12* (MO). SUCRE: Cerro Espejo, peninsula de Paria, *Steyermark & Rabe 96072* (G, K, NY, US).

*Pleurothyrium costanense* is known from the Cordillera de La Costa, the Sierra de San Luis in Edo. Falcón, and the Venezuelan Andes, where it occurs between 700 and 2,200 m elevation. Most collections are from about 1,000 m. Only one other *Pleurothyrium* species, *P. steyermarkianum* Allen, is known from the Venezuelan Andes, but this species lacks the erect-tomentose pubescence on the lower leaf surface and the young twigs. *Pleurothyrium trianae* is not uncommon at the base of the Andes and Cordillera de La Costa, but this species differs greatly from *P. costanense* in the reflexed margins of the tepals and the dense, but short tomentellous indument on the lower leaf surface, which completely covers the leaf surface.

There is a good deal of variation in the color of the indument in *P. costanense*. Especially the type and *Steyermark 96072* have a light color of indument, whereas some of the other collections are dark ferruginous. In other characters, such as leaf shape, type of indument, raised tertiary venation, and the short, densely pubescent style, these collections agree with each other, and consequently all are placed in the same species.

**Pleurothyrium crassitepalum** van der Werff, sp. nov. TYPE: Colombia. Valle: Río Naya near Puerto Merizalde, elev. 5–20 m, *Cuatrecasas 13986* (holotype, F; isotype, US). Figures 17, 18.

Arbor magna. Ramuli teretes vel subangulares, foliorum cicatribus magnis praediti, hornotini dense, minute, adpresse fusco-pubescentes, annotini glabrescentes. Gemma terminalis dense, adpresse avellino-pubescens. Folia ad apices ramulorum congesta, firme chartacea, elliptica vel elliptico-obovata, 10–17 × 6–9 cm, basi attenuata vel cuneata, apice rotundata vel obtusa, supra glabra, subtus indumento minuto, fere papilloso, praedita; nervis lateralibus 13–16 utroque costae latere, versus marginem sursum curvatis et in dimidio distale folii venam superiorem junctis; supra venatione immersa, subtus costa, nervis lateralibus et venatione tertia elevata. Petioli 11–17 mm longi, ca. 3 mm diametro. Inflorescentiae ex axillis bractearum ortae, dense fusco-tomentulosae, 7–14 cm longae, plerumque racemosae, aliquando ramulis cymae more divisis. Pedicelli 5–11 mm longi, fusco-tomentulosi. Flores extus rufescentes, intus albidi fide coll., ca. 13 mm diametro. Tepala 6, subaequalia, late ovata, exteriora ca. 5 mm longa, interiora ca. 4 mm longa, dense fusco-tomentella in sicco, crassa. Stamina 9, 4-locellata, locellis lateralibus, antheris papillosis, glandulis magnis connatis stamina cingentibus. Ovarium glabrum, ellipsoideum, ca. 1 mm longum, style glabro, ca. 1.5 mm longo, stamina non superante. Tubus floralis glaber. Fructus ignotus.

Large tree, Twigs solid, terete or somewhat angular, with large scars of old leaves, the tips densely, but minutely, brown appressed pubescent, glabrescent on older parts, 5–6 mm diam. 5 cm below apex. Terminal bud with a dense, appressed tan pubescence. Leaves clustered near the tips of branches, firmly chartaceous, elliptic to elliptic-obovate, 10–17 × 6–9 cm, the base attenuate or cuneate, the tip rounded or obtuse, the upper surface glabrous, the lower surface covered with a short, minute, almost papillose indument; lateral veins 13–16 on each side, arching upwards near the margin and connected with the superior vein in the upper half of the lamina, the marginal vein well-developed; venation immersed on the upper surface, but midrib, lateral veins and tertiary venation raised on lower surface. Petioles 11–17 mm long, flattened on the upper side, ca. 3 mm in diameter, with a similar indument as twigs. Inflorescences in axils of cataphylls near the tips of branches, densely brown-tomentulose, 7–14 cm long, mostly racemose, but occasionally with branchlets once cymosely branched, with 10–20 flowers, bracts not present at anthesis. Pedicels 5–11 mm long, densely brown tomentulose. Flowers dark reddish brown outside, white inside fide collector, ca. 13 mm diam. Tepals 6, subequal, all

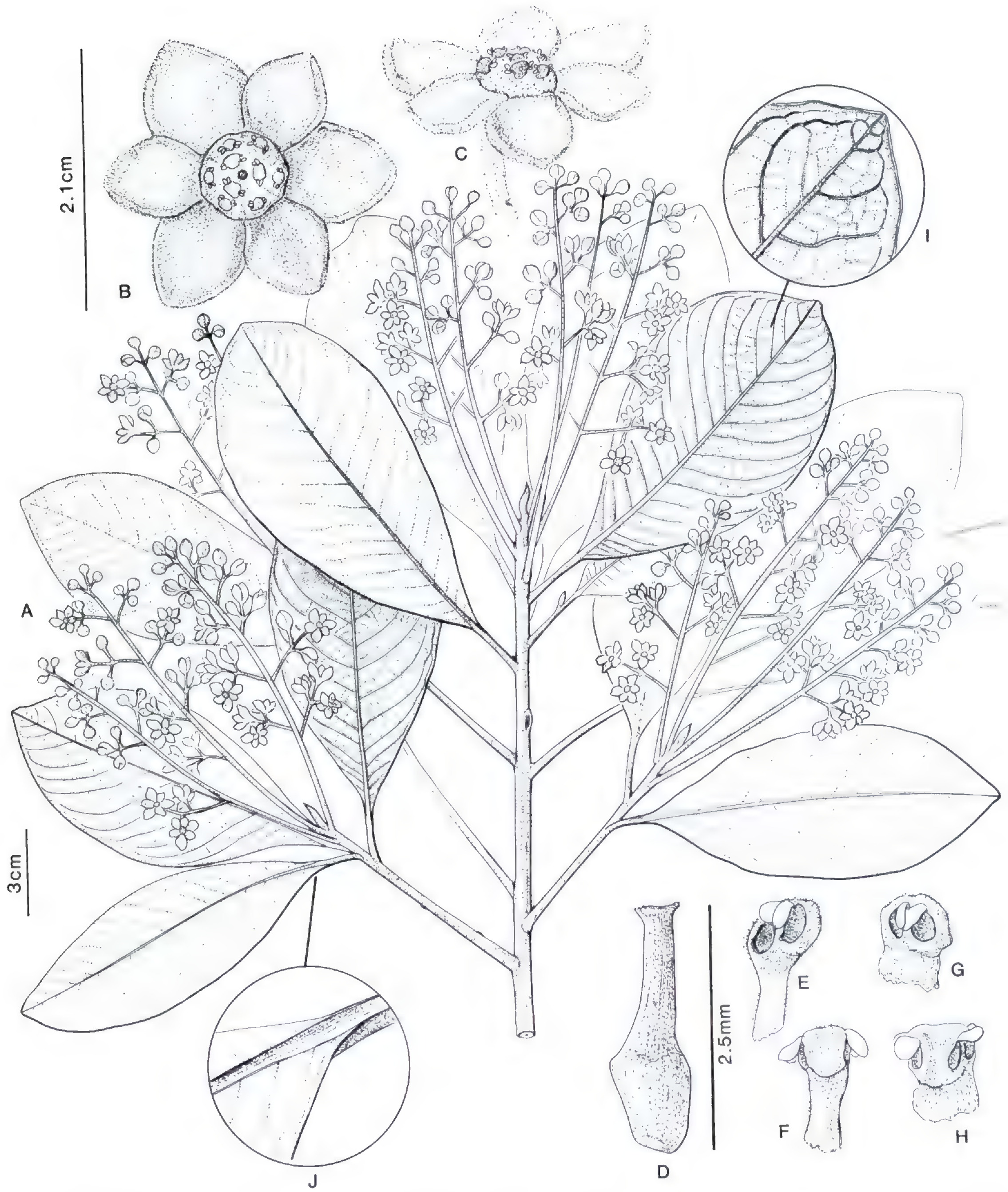



FIGURE 17. *P. crassitepalum.*—A. Habit.—B, C. Flowers.—D. Pistil.—E, F. Lateral and frontal view of outer stamen.—G, H. Lateral and frontal view of inner stamen.—I. Detail of lower leaf surface.—J. Base of leaf.

broadly ovate, the outer 3 ca. 5 mm long, the inner 3 ca. 4 mm long, all on both surfaces densely brown tomentellous, thick. Stamens 9, all 4-celled, the cells lateral and opening back-to-back, the anthers papillose; glands strongly enlarged, forming a central dome, enclosing the outer anthers and fused. Ovary glabrous, ellipsoid, ca. 1 mm long, style glabrous, ca. 1.5 mm long, not surpassing stamens; stigma not or hardly enlarged. Floral tube glabrous. Fruit unknown. Flowers: February. Elevation range: 5–20 m.

*Collection studied.* COLOMBIA: VALLE: Puerto Merizalde, Río Naya, Costa del Pacifico, *Cuatrecasas 13986* (F, US).

*Pleurothyrium crassitepalum* is one of several *Pleurothyrium* species known only from the type. Distinctive characters are the thick tepals, which

FIGURE 18. Distribution of *P. crassitepalum* (★), *P. giganthum* (●), *P. glabrifolium* (○), and *P. golfodulcense* (■).

appear almost double-margined, the very short and dense pubescence on the leaves, which is unusual in the group of species with large flowers and relatively few-flowered inflorescences, and the raised tertiary venation on the lower leaf surfaces. The clustered leaves with rounded tips are also useful characteristics. Common names for this species are nadde, nande, and palo blanco. The wood is used for making boards.

**Pleurothyrium cuneifolium** Nees, Syst. Laur.: 352. 1836. *Ocotea triangulata* Kostermans, J. Sci. Res. (Jakarta) 1: 122, 1952. TYPE: Brazil. Amazonas: Tefé (Ega), *Poeppig 2908* (holotype not designated; B, G—2 sheets, GZU, LE). Figures 19, 20.

*Pleurothyrium chrysophyllum* Nees, Syst. Laur.: 351. 1836. SYNTYPES: Peru. Cuchero, *Poeppig 1718* (B, as no. 1719, GZU, LE, US); Peru. Chachapoyas, Yambrasbamba, *Matthews 1432* (E, K).

*Pleurothyrium macranthum* Nees, Linnaea 21: 512. 1848. SYNTYPES: Peru. *Poeppig 1790* (not seen); *Poeppig 2125* (G, LE).

Tree, to 20–25 m. Twigs angular or ridged when young, becoming ± terete with age, often fistulose, often lenticellate, the young parts minutely tomentellous, glabrescent with age; diameter of young twigs 4–8 mm, depending on how strongly fistulose the twigs are. Terminal bud densely brown tomentellous. Leaves alternate, chartaceous, (narrowly) elliptic to (narrowly) elliptic-obovate, 15–30 × 7–15 cm, the base cuneate, acute or abruptly rounded, the tip obtuse or acute, lateral veins 12–18 on each side, arching upward near the margin and weakly loop-connected in the distal half of the lamina, immersed on the upper surface, midribs and lateral veins raised on lower surface, upper surface glabrous or nearly so, lower surface glabrous, papillose or tomentellous, the indument wearing off with age. Petioles 1.3–2.0 cm long, canaliculate, with similar indument as twigs. Inflorescences in axils of cataphylls, or infrequently in

FIGURE 19. *P. cuneifolium*.—A. Habit.—B. Detail of normal inflorescence.—C. Stunted inflorescence with main axis inhabited by ants.—D. Androecium and glands.—E. Pistil.—F. Young fruits.—G. Hollow twig, showing holes used by ants.

FIGURE 20. Distribution of *P. cuneifolium* (★) and *P. glabritepalum* (●).

axils of normal leaves, brown-tomentellous, 10–27 cm long, the lateral branchlets to four times cymosely branched but sometimes (when inflorescence fistulose) reduced to short spurs with clustered flowers, many-flowered, bracts often persistent during anthesis, ovate, to ca. 5 mm long, tomentellous on both surfaces. Pedicels of variable length, the lateral flowers of a cyme often nearly sessile, but flowers on fistulose inflorescences with pedicels of up to 7 mm long, with same indument as inflorescence. Flowers white, yellow to yellowish red, from 7 to 14 mm diam. Tepals 6, equal, ± erect, elliptic or elliptic-ovate, 3–7 mm long, the outer 3 (minutely) tomentellous outside, inner 3 with a basal, triangular, (minutely) tomentellous patch, otherwise glabrous, all tepals glabrous inside (rarely papillose), the margins plane or inrolled, not reflexed. Stamens 9, 4-celled, the lower 2 cells lateral-extrorse, the upper 2 lateral-introrse; glands strongly enlarged, surrounding the base of the outer stamens, fused. Pistil 2–3 mm long, the ovary about as long as the style or slightly shorter, sometimes well defined, sometimes gradually narrowed into the style, the lower ⅓–⅔ glabrous, the remainder (and the style) papillose, the stigma often platelike. Floral tube glabrous inside, rarely pubescent. Cupule cup-shaped, (sometimes?) with 6 thick lobes, warty, ca. 2 cm wide, 1 cm high. Fruit ovoid, ca. 2 cm long. Fruits: February–March. Flowers: nearly year-round. Elevation range: 100–1,800 m.

*Collections studied.* BRAZIL. AMAZONAS: ad Ega (= Tefé), *Poeppig 2908* (G); near Rio Chipurana, *Huber 1557* (G). COLOMBIA: ANTIOQUIA: Anori, Planta Providencia, *Shepherd 537* (MO); Mpio. de San Carlos, near ISA hydro-electric dam, *McPherson 13365* (MO); Mpio. de San Luis, sector Río Samana–Río Claro, vereda Tulipan, *Cogollo 170* (MO). BOYACA: El Humbo, 130 mi. N of Bogotá, *Lawrance 780* (A, F, G, UC, US). HUILA: *Little 8488* (A). ECUADOR: MORONA-SANTIAGO: along new road Mendez–Morona, *van der Werff 11157* (MO). NAPO: 8 km Río abajo de Misahualli, *Neill 7019* (F, K, MO), *Neill 7128* (MO). PERU: CUCHERO: *Poeppig 1718* (US); Peruvia subandina, *Poeppig 1845* (G), *Poeppig 2125* (G). AMAZONAS: Quebrada de Bashuchunuk, *Kayap 145* (F, G, MO); Quebrada Kayamas, Río Cenepa, *Kayap 648* (MO). CHACHAPOYAS: Yambrasbamba, *Matthews 1432* (E, K). CUZCO: Hda. Santa Rosa (Convención), *Soukop 910*

(F). JUNIN: Chanchamayo, Mina Pichita, above San Ramon, *van der Werff 8673* (MO); Oxapampa, Chontabamba, *Smith 3061* (MO). LORETO: Quistococha, *Ayala 574* (MO); Fortaleza, near Yurimaguas, *Klug 2779* (A, F, G, GH, K, MO, S, US); Balsapuerto, *Klug 2931* (A, F, G, GH, K, S); Cachipuerto, Río Cachiyacu, *Klug 3116* (A, F, G, GH, K, MO, S, US); Pumayacu, between Balsapuerto and Moyabamba, *Klug 3195* (A, F, G, GH, K, MO, NY, S), *Klug 3228* (A, F, G, GH, K, MO, NY, S, US); La Victoria on the Amazon River, *Williams 2715* (F). MADRE DE DIOS: Tambopata, *Gentry 45760* (MO); Tambopata Nature Reserve, *Gentry 57817* (MO); Tambopata, Cuzco Amazonico Lodge, *Nuñez 12207* (MO). PASCO: Palcazu Valley, *Hartshorn 2631* (MO); Palcazu Valley, Buenos Aires, *Hartshorn 2937* (MO); Oxapampa, Huancabamba, *Reynel 102* (MO); Oxapampa, Chontabamba valley, 2–8 km W of Oxapampa, *Gentry 39902* (MO); Oxapampa, Distr. Iscozacin, Palcazu valley, *Pariona 63* (MO); Oxapampa, Chontabamba, 2 de Mayo, *Smith 1743* (G, MO), *Smith 1756* (G, MO); Oxapampa, Villa Rica, *van der Werff 8266* (MO), *van der Werff 8287* (MO); Oxapampa, Villa Rica, Santa Polonia Alta, *van der Werff 8291* (MO); Oxapampa, near Oxapampa, *van der Werff 8346* (MO). SAN MARTIN: Zepalacio, near Moyabamba, *Klug 3567* (F, G, GH, MO, NY, S, US). UCAYALI: Distrito Inahuaya, Comunidad de Santa Rosa, *Campos 364* (MO); 65 km NE of Pucallpa, *Gentry 58574* (MO).

As accepted here, *P. cuneifolium* is a wide-ranging species, known from Colombia, Ecuador, Peru, and Brazil, and occurs in the Amazonian lowlands and up to 1,800 m in the Peruvian Andes. Given its wide distribution and presence in different habitats, it is not surprising to find that it is a variable species. The two species placed in synonymy under *P. cuneifolium*, *P. chrysophyllum* and *P. macranthum*, were not published at the same time by Nees and he did not discuss the characters that separate the three species. Meissner (1864) regarded *P. chrysophyllum* as scarcely more than a variety of *P. cuneifolium*, differing in a denser indument, slightly smaller flowers, shorter pedicels, more branched inflorescences, and flowers with a linear bract near their base. *Pleurothyrium macranthum* differed, fide Meissner (1864), in its larger flowers. Mez (1889) placed *P. macranthum* under *P. cuneifolium*, but kept *P. chrysophyllum* apart; he separated the two on the relative length of the style and ovary: the style longer than the ovary in *P. cuneifolium* and shorter in *P. chrysophyllum*. I found this not a reliable character: in most flowers I dissected the style was about as long as the ovary, and it seemed that often in old flowers the apical part of the style and the stigma had fallen off, which makes it unsuitable as a character to separate two taxa. MacBride (1938) did not mention *P. macranthum* and separated *P. cuneifolium* and *P. chrysophyllum* by the density of their indument on the leaves. The denser indument occurs mostly on specimens from higher elevations, such as the syntypes of *P. chrysophyllum* and several collections from the Oxapampa area (1,500–1,800 m), but *Ayala 574* (Quistacochas, near Iquitos, 140 m) is equally tomentellous. Because minutely tomentellous specimens have been collected near Oxapampa and in the lowlands, and no other characters are restricted to the collections with denser indument, I reduce *P. chrysophyllum* to synonymy. The larger number of collections now available show that there are no discontinuities in flower size, and thus *P. macranthum* cannot be recognized as a distinct taxon. The largest flowers, with tepals to 7 mm long, are found on three Klug collections (*3195*, *3228*, and *3567*), which have strongly fistulose branches and fistulose inflorescences. The branchlets of the inflorescences have, in these collections, been reduced to short spurs bearing a cluster of flowers. This inflorescence shape is quite similar to that of the type of *P. poeppigii* and, indeed, the Klug collections had in some herbaria been annotated as *P. poeppigii*. However, the flowers of *P. cuneifolium* are clearly larger, lack reflexed margins of their tepals, and are glabrous on the inner surface of the tepals.

Included in *P. cuneifolium* are a few collections with entirely glabrous leaves, for instance, *Lawrance 780. Neill 7019* provides the link between the collections with glabrous leaves and tomentellous leaves; it has young, tomentellous and older, glabrous leaves.

Unfortunately, fruiting material of this species it not well known. A common name in the Oxapampa region is roble zapallo, because the cupule has six thick ribs, like the ribs on a squash. This is both unusual for Lauraceae and easy to see on fresh material, but disappears largely on dried specimens. It seems that this cupule type also occurs in lowland populations (Palcazu valley). Flowering material of the roble zapallo fits very well in *P. cuneifolium*.

Infrequently found in Lauraceae are the strikingly lenticellate twigs of many collections of *P. cuneifolium*; other useful characters for *P. cuneifolium* are the fistulose twigs, tomentellous inflorescences, (usually) glabrous inner face of tepals, and the more or less erect tepals (especially the inner ones) at anthesis. Although *P. cuneifolium* lacks reflexed margins of the tepals, I do not think its closest relatives are among the other species with plane tepals. Leaf shape, venation, the more or less erect tepals, and indument of the pistil all suggest a relationship with the species with reflexed margins of tepals, such as *P. trianae* and *P. poeppigii*. Probably also closely related is *P. obovatum*,

a species with fistulose twigs (and sometimes fistulose inflorescences), more or less erect tepals at anthesis, and some lenticels on the small piece of twig I have seen.

A few specimens of *Pleurothyrium cuneifolium* lacked a fistulose stem and would key to *P. trianae*, while very few collections of *P. trianae* had a fistulose stem and would key to *P. cuneifolium*. Apart from the characters used in the key, these two species can be separated as follows: *P. cuneifolium* has longer tepals (3–7 mm vs. ca. 2 mm), larger and more persistent bracts protecting the flower buds, and has the inner surface of the tepals usually glabrous (papillose in *P. trianae*).

**Pleurothyrium giganthum** van der Werff, sp. nov. TYPE: Ecuador. Los Ríos: Río Palenque Science Center, km 56 Quevedo–Sto. Domingo, *Dodson 18217* (holotype, QCNE). Figures 18, 21.

Arbor, ad 30 m alta. Ramuli angulares, solidi, fusco-tomentosi, cicatricibus conspicuis et plerumque cataphyllis adpressis praaediti. Cataphylla 1–2.5 cm longa. Gemma terminalis fusco-tomentosa, ad 7 mm longa. Folia ad apices ramulorum aggregata, chartacea, 30–60 × (10–)15–24 cm, obovata vel obovato-elliptica, sensim versus basim attenuata, basi rotundata, apice apiculata vel rotundata; supra costa nervisque fusco-pubescentibus, lamina pilis paucis erectis, maturitate deciduis praedita, infra costa nervisque fusco-tomentosis, lamina pilis erectis praedita; nervis lateralibus 15–20 utroque costae latere, supra immersis, subtus costa nervisque elevatis, reticulatione minus elevata; venatione in dimidio distale brochidodroma. Petioli crassi, fusco-tomentosi, 5–10 mm longi. Inflorescentiae ex axillis cataphyllorum ortae, foliis perbreviores, fusco-tomentosae, racemosae. Flores virides. Tepala 6, subaequalia, tres interiora basi magis angustata, omnia margine albida, intus et extus pubescentia. Stamina nova, glandulis magnis connatis stamina cingentibus. Ovarium et receptaculum glabrum. Fructus immaturus in cupula inclusus; cupula immatura hexangularis, lenticellata, sensim in pedicello attenuata.

Tree, to 30 m tall. Twigs roundly angular, solid, brown-tomentose, diameter 7–9 mm ca. 5 cm below the tip with conspicuous scars of fallen leaves, often with cataphylls at the base of the most recent growth, these cataphylls appressed and 1–2.5 cm long. Terminal bud brown-tomentose, ca. 7 mm long, narrower than the twig. Leaves clustered near the tips of the branches, chartaceous, 30–60 × (10–)15–24 cm, obovate or obovate-elliptic, gradually narrowed toward the base, the base abruptly rounded, the tip shortly acute to rounded, lateral veins 15–20 on each side, immersed on the upper surface, the midrib strongly raised on the lower surface, lateral veins and tertiary venation also raised on lower surface; lateral veins arching upward near the margin and becoming loop-connected in the distal half; upper surface drying dark green, with brown-tomentose pubescence along the midrib, less so along the lateral veins, the lamina with scattered, erect hairs, which wear off with age; lower surface with brown-tomentose midrib and lateral veins, the lamina with erect hairs, which leave the surface readily visible. Petioles brown-tomentose, 5–10 mm long and 4–6 mm thick. Inflorescences racemose, in the axils of cataphylls below the leaves, ca. 6 cm long, much shorter than the leaves, brown-tomentose, the flowers subtended by brown-tomentose bracts ca. 5 mm long. Pedicels ca. 1.2 cm long, brown-tomentose, gradually widened toward the buds, 3-angled, the ridges continuing as a low keel on the 3 outer tepals. Flowers ca. 2 cm diam., light green with whitish margins. Tepals 6, subequal, the outer 3 ca. 10 × 9 mm, the inner 3 ca. 7 × 7 mm, more constricted at their base than the outer 3, broadly ovate to broadly elliptic, pubescent on both surfaces. Stamens 9, the valves back to back, glands strongly enlarged, completely enclosing the stamens and fused. Ovary (in young fruit) subglobose, glabrous; floral tube glabrous inside. Young fruits fully enclosed in cupule, this lenticellate, gradually narrowed into pedicel, ca. 2.5 cm long, and strongly 6-angled. Fruits: May. Flowers: January, September.

*Collections studied.* ECUADOR. LOS RIOS: Rio Palenque Science Center, *Dodson 10181* (MO), *van der Werff 12362* (MO); Rio Palenque Science Center, *Dodson 13632, 18217* (both QCNE), *Dodson 6302, van der Werff 9471* (both MO).

*Pleurothyrium giganthum* is only known from one or two trees at the Río Palenque Science Center. Characteristic for this species are the large, clustered leaves, the conspicuous cataphylls, and the erect pubescence on the lower leaf surface. This species was first collected flowering in January 1983, but the collected flowers were later lost. Immature fruits were collected in May 1987, also indicating January–February as the flowering season. Since 1987, C. Dodson regularly checked the only known tree for flowers and finally, in September 1990, the tree became deciduous and flowered briefly when the new foliage developed.

The specific epithet is based on the Greek words gigas (giant) and anthos (flower) and refers to the very large flowers of this species.

This species was included in the *Flora of Río Palenque* (Dodson & Gentry, 1978) as *Ocotea* sp. nov.

**Pleurothyrium glabrifolium** van der Werff, sp. nov. TYPE: Ecuador. Napo: Río Payamina, 2–10 km S of the road Coca–Loreto, *Cerón*

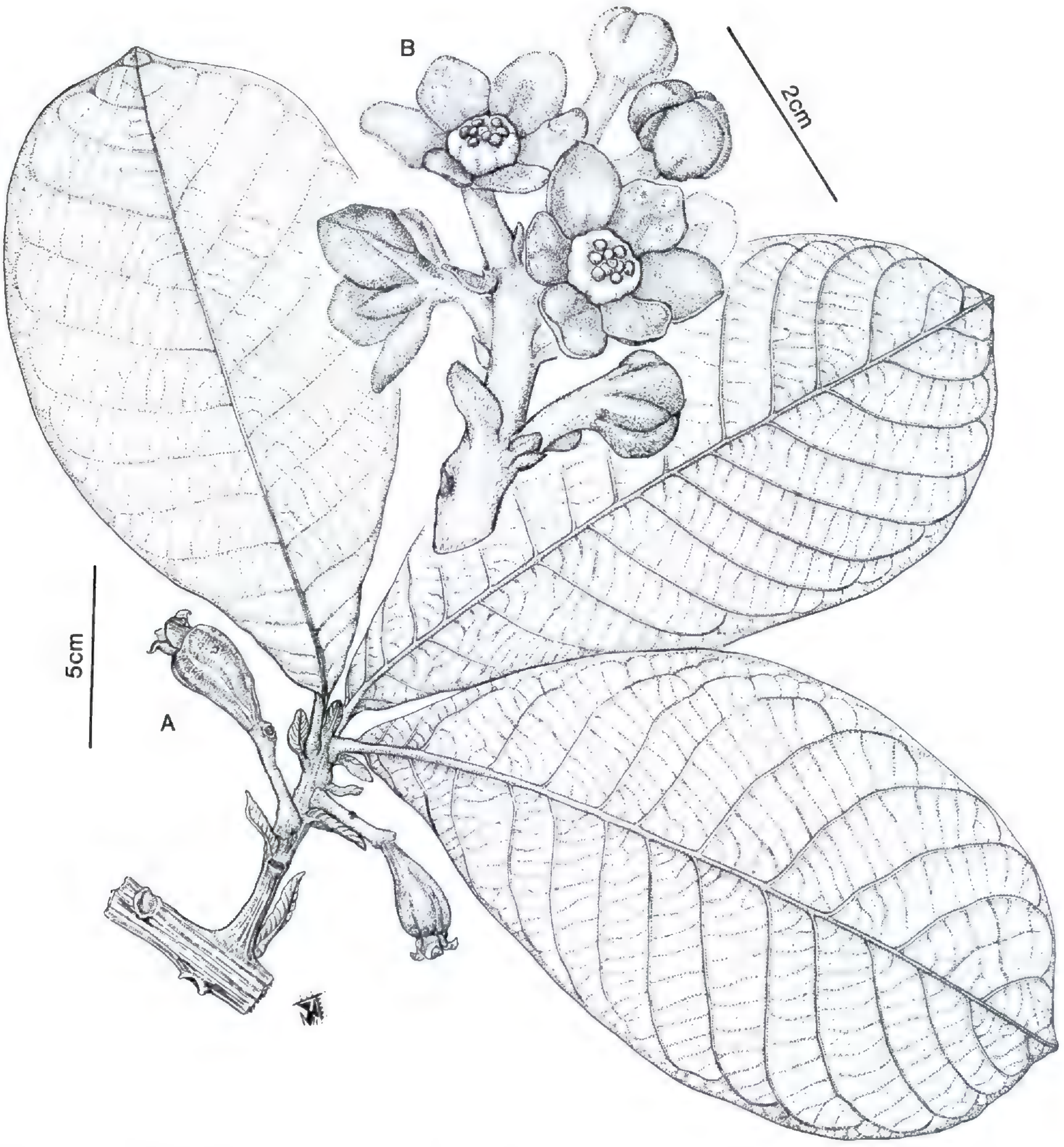



FIGURE 21. *P. giganthum*.—A. Habit.—B. Inflorescence.

*& Palacios 3017* (holotype, MO; isotypes, AAU, C, COL, G, HBG, K, LE, NY, QAME, QRS, U, US). Figures 18, 22.

Arbor, ad 15 m. Ramuli teretes, solidi, ad apicem brunneo-tomentosi, glabrescentes. Gemma terminalis brunneo-tomentosa. Folia alterna, subcoriacea, elliptica, 14–25 × 6–9 cm, basi acuta, apice acuminata, glabra; supra glanduloso-punctata, venatione immersa; subtus costa nervisque elevatis, reticulatione paullo elevata; nervis utroque costae latere 12–16, in dimidio distale venatione brochidodroma. Petioli 1.5–3 cm longi, canaliculati, indumento ramulis similes. Inflorescentiae ex axillis bractaerum ortae, 7–16 cm longae, brunneo-tomentellae, paniculatae, bracteis ad anthesim deciduis. Flores 6–7 mm diametro. Tepala 6, aequalia, ovata, ca. 3 mm longa, 3 exteriora extus tomentella, intus glabra, 3 interiora extus basi tomentella, demum glabra, intus glabra. Stamina 9, 4-locellata, locellis lateralibus, filamentis quam antheris brevioribus; glandulis magnis, connatis, stamina cingentibus. Pistillum glabrum, 1 mm longum, stylo breve, stigmate peltata. Receptaculum glabrum. Fructus ignoti.

Tree, to 15 m tall. Twigs terete, solid, the very tip and terminal bud brown-tomentose, older parts becoming glabrous, ca. 4 mm diam. 5 cm below apex. Leaves alternate, subcoriaceous, elliptic, 14–25 × 6–9 cm, the base acute, tip acuminate, glabrous on both surfaces, the upper surface gland-dotted, venation immersed on upper surface, costa and lateral veins raised on lower surface, the tertiary venation less so; lateral veins 12–16 on each side, curving upward near the margin and becoming loop-connected in the distal half of the lamina. Petioles 1.5–3 cm long, canaliculate, with similar tomentum as the twig. Inflorescences in axils of cataphylls, 7–16 cm long, brown-tomentellous, pa-

FIGURE 22. *P. glabrifolium.*—A. Habit.—B. Flower.—C. Cross section of flower.—D. Detail of inflorescence.—E. stamen.—F. Pistil.

niculate, many-flowered, the branchlets 1–2 times cymosely branched, bracts mostly deciduous at anthesis. Pedicels 2–3 mm long, brown-tomentellous. Flowers 6–7 mm diam., whitish. Tepals 6, equal, ovate, ca. 3 mm long, tomentellous outside, but inner 3 with glabrous margin and tip; glabrous inside. Stamens 9, glabrous, 4-celled, the cells lateral; filaments shorter than the anthers, ca. 0.2 mm long; glands enlarged, fused, completely enclosing the stamens. Pistil glabrous or nearly so, ca. 1 mm long, the style very short, stigma platelike. Floral tube shallow, glabrous; ovary largely covered by the enlarged glands. Fruits unknown. Flowers: December. Elevation range: 250–300 m.

*Collections studied.* ECUADOR. NAPO: Río Payamino, 2–10 km S of Carretera Coca–Loreto, *Ceron & Palacios 3017* (AAU, C, COL, G, HBG, K, LE, MO, NY, QAME, QRS, U, US); El Chuncho, 6 km from Río Payamino, *Palacios 2288* (MO).

*Pleurothyrium glabrifolium* is only known from two collections, made in the same area in the lowlands of eastern Ecuador. The combination of glabrous inner surface of tepals, glabrous and alternate leaves is characteristic for this species. The only other Amazonian species with the inner surface of the tepals glabrous is *P. panurense*, but that species has clustered leaves with a minute, whitish, and dense indument on the lower leaf surface. The completely glabrous stamens and pistil of *P. glabrifolium* are an uncommon character in *Pleurothyrium*.

**Pleurothyrium glabritepalum** van der Werff, sp. nov. TYPE: Colombia. Choco: hills behind Bahia Solano (Puerto Mutis), *Gentry & Forero 7201* (holotype, MO; isotypes, HBG, U). Figures 20, 23.

Arbor, ad 8 m alta. Ramuli solidi, teretes, porphyreo-tomentosi, glabrescentes. Gemma terminalis parva, porphyreo-tomentosa. Folia alterna, subchartacea, elliptica, 10–18 × 3.5–6 cm, basi acuta, apice acuminata, acumine 1–2 cm longo, supra glandulo-punctata et pilis dispersis praedita sed secus costam nervosque laterales indumento densiore, subtus pilis subdispersis arrectis praedita, indumento paginam non tegente, sed secus costam nervosque tomentoso. Nervi laterales 5–8 utroque costae latere, venatione brochidodroma in dimidio distale, supra immersa subtus costa nervisque elevatis, venatione tertia paullo elevata. Petioli 10–15 mm longi, teretes. Inflorescentiae ex axilis bractearum ortae, 2–4 cm longae, 1–3-florae, porphyreo-tomentosae, sub anthesi bracteis deciduis. Flores ca. 13 mm diametro. Tepala 6, subaequalia, ovata, 3 exteriora 5.5 mm longa, extus tomentulosa, intus glabra, 3 interiora 4.5 mm longa, extus basi tomentulosa, demum glabra, intus glabra. Stamina 9, glabra, 4-locellata, locellis lateralibus, glandulis incrassatis stamina cingentibus, coalitis, ovarium depresse globosum, glabrum, ca. 1 mm diametro, tubus floralis glaber. Fructus ignotus.

Tree, at least 8 m tall fide collectors. Twigs solid, terete, brown-tomentose when young, glabrescent, 2–3 mm diam. ca. 5 cm below the tip. Terminal bud small, brown-tomentose. Leaves alternate, thinly chartaceous, elliptic, 10–18 × 3.5–6 cm, the base acute, the tip acuminate, the acumen 1–2 cm long, the upper surface with gland dots and scattered brown hairs, these much denser along midrib and lateral veins, the lower surface with a rather sparse, erect pubescence, the hairs somewhat wrinkled and not covering the leaf surface; indument brown-tomentose along midrib and lateral veins; lateral veins 5–8 on each side, venation immersed on upper surface, midrib and lateral veins raised on lower surface, the tertiary venation slightly so, lateral veins arching upward near the margin and weakly loop-connected in the distal half of the lamina. Petioles 10–15 mm long, terete, with similar pubescence as twigs. Inflorescences in axils of cataphylls, 1–3-flowered, 2–4 cm long, brown-tomentose, bracts lacking at anthesis. Pedicels 4–5 mm long, tomentose. Flowers green with tan center (fide collectors), ca. 13 mm diam. Tepals 6, subequal, the outer three 5.5 mm long, the inner three 4.5 mm long, the outer three tomentulose outside, inner three with a basal, triangular tomentulose patch, otherwise glabrous; all tepals with a glabrous inner surface. Stamens 9, 4-celled, glabrous, the cells lateral and opening back-to-back, glands strongly enlarged, surrounding the stamens, fused; ovary depressed globose, glabrous, ca. 1 mm diam., receptacle glabrous inside. Fruit unknown. Flowers: January. Elevation range: below 250 m.

*Collection studied.* COLOMBIA. CHOCO: hills behind Bahia Solano (Puerto Mutis), *Gentry & Forero 7201* (HBG, MO, U).

*Pleurothyrium glabritepalum*, named after the glabrous inner surface of the tepals, is only known from the type collection. Useful characters for its identification are the following: the more or less erect pubescence, which is also present on the upper leaf surface, the gland dots on the upper leaf surface, the alternate, acuminate thin leaves, the few-flowered inflorescences, and the glabrous inner surface of the tepals. The leaves have, for the genus, few lateral veins and a marginal vein is weakly developed.

**Pleurothyrium golfodulcense** Burger & Zamora, Fieldiana Botany, New Series, 23: 115.

FIGURE 23. *P. glabritepalum.*—A. Habit.—B. Flower.—C. Leaf base, showing indument.—D. Leaf apex.

1990. TYPE: Costa Rica. Puntarenas: Alto de las Mogas, *Sanchez, Zamora & Brenes 1228* (holotype, CR not seen; isotype, F not seen). Figures 18, 24.

Tree, to 15 m tall. Twigs terete, solid, gray pubescent, 2–3 mm diam. ca. 5 cm below tip. Terminal bud densely gray-pubescent. Leaves alternate, thinly chartaceous to coriaceous, 10–20 × 4–7 cm, elliptic to elliptic-obovate, base acute or obtuse, apex acuminate, acumen to 2 cm long, upper surface glabrous, except for the ± pubescent midrib, gland-dotted, lower surface glabrous or with minute appressed hairs, but midrib and to a lesser degree lateral veins pubescent; lateral veins 6–9; loop-connected in distal half of lamina, venation immersed on upper surface, midrib and lateral veins raised on lower surface. Petioles 6–22 mm long. Inflorescences in axils of cataphylls or normal leaves, to 10 cm long, racemose, ferruginous pubescent, the lateral branches often subtended by an elliptic bract, to 6 mm long, pubescent on both surfaces; pedicels to 14 mm long, often with a bracteole halfway between inflorescence axis and flower. Flowers white, rotate, 9–12 mm diam. Tepals 6, equal, elliptic, 4–6 mm long, ca. 3 mm wide, gray to ferruginous pubescent outside, papillose inside. Stamens 9, 4-celled, the cells lateral to apical, opening back-to-back, the glands strongly enlarged and, together with the stamens, forming a dome 2.5 mm wide and 1 mm high, the glands enclosing the stamens, but not fully fused. Pistil 2.2 mm

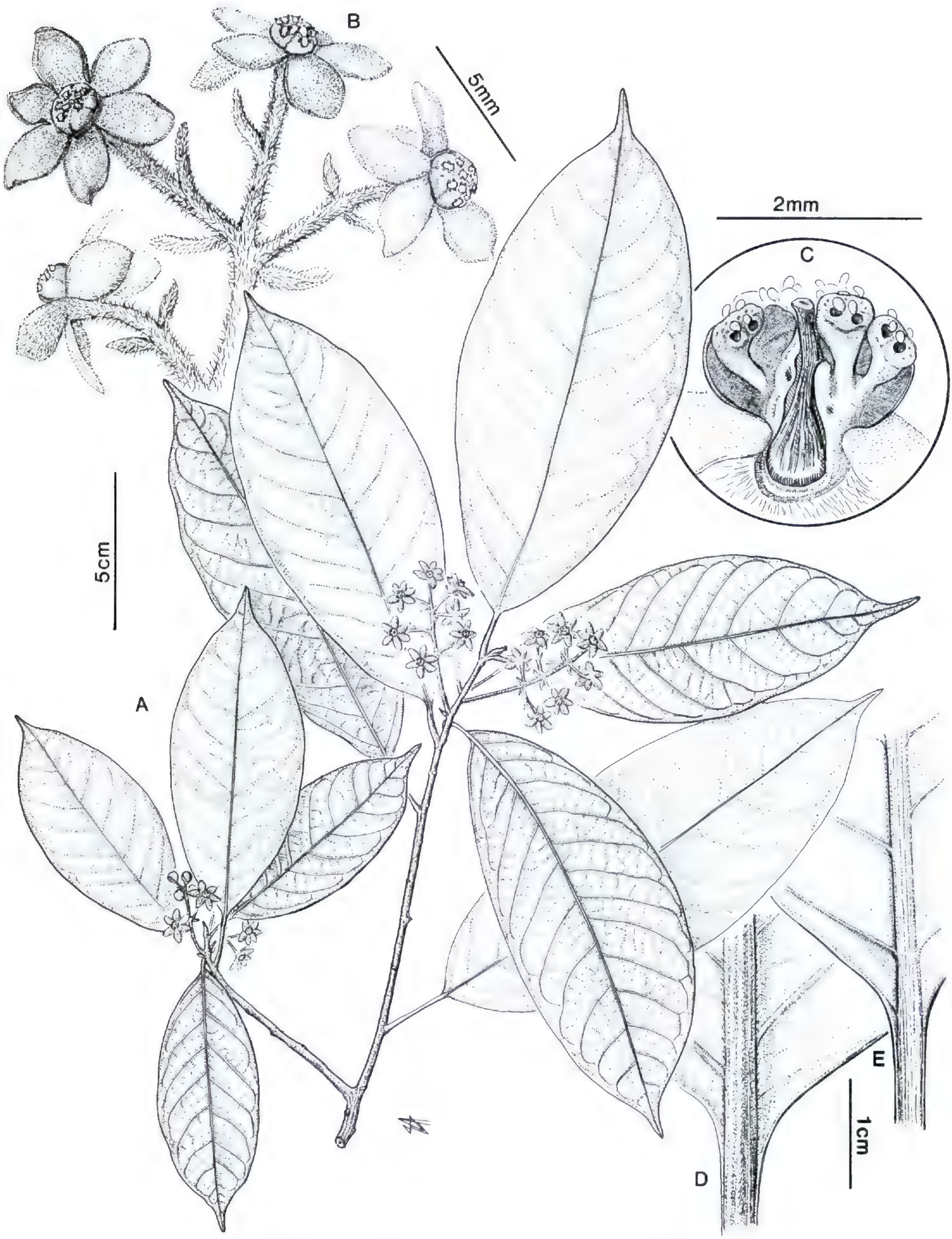



FIGURE 24. *P. golfodulcense.*—A. Habit.—B. Part of inflorescence.—C. Cross section of flower.—D, E. Lower and upper surface of leaf base.

long, ovary ca. 1 mm long, pubescent, style sparsely pubescent. Receptacle pubescent inside. Cupule with coarse warts, 2 cm tall, 2 cm wide. Fruit unknown. Flowers: January–February. Elevation range: 200–800 m.

*Collections studied.* COSTA RICA. PUNTARENAS: forested slopes above Golfito, *Burger 4690* (CR, F, MO). PUNTARENAS: forested hills above Palmar Norte, *Allen 5885* (GH, UC); Parque Nacional Corcovado, Los Patos Forest, *Kernan 184* (CR, MO), *Kernan 187* (CR, MO); Osa, Rancho Quemado, *Jimenez 648* (MO).

*Pleurothyrium golfodulcense* is restricted to the Osa peninsula and adjoining area in Costa Rica. I have accepted a rather wide concept of this species and include here, for instance, *Kernan 184*, which differs from typical *P. golfodulcense* in its thinner leaves, shorter petioles and gray vs. ferruginous pubescence. In leaf size and shape, venation, pubescent pistil and receptacle, gland-dotted leaves, petiole length, and bracts pubescent on both surfaces it fits in *P. golfodulcense*, and because it was collected together with typical *P. golfodulcense* (*Kernan 187*) and young leaves of *Allen 5885* are as thin as those of *Kernan 184*, I prefer to include *Kernan 184* in *P. golfodulcense*.

The closest relatives of *Pleurothyrium golfodulcense* are probably the Panamanian species *P. racemosum* and *P. pilosum* and the Ecuadorian-Colombian *P. tomiwahlii* (see discussion under *P. tomiwahlii*).

**Pleurothyrium grandiflorum** van der Werff, Ann. Missouri Bot. Gard. 74: 408. 1987. TYPE: Colombia. Chocó: Río Mecana, *Juncosa 1675* (holotype, MO). Figures 25, 26.

Tree, 15 m. Twigs ridged, becoming terete, solid, very finely appressed puberulent, ca. 3 mm diam. 5 cm below the tip. Terminal bud appressed puberulent, shiny. Leaves alternate, thinly chartaceous, 15–24 × 4–7 cm, elliptic or narrowly elliptic, the base sharply acute or slightly decurrent on petiole, the tip acute, the upper surface nearly glabrous, but with some fine appressed hairs, especially on the midrib; the lower surface with scattered, minute, appressed hairs, these more numerous along lateral veins and midrib; venation on upper surface immersed, but slightly raised on lower surface; lateral veins 15–20 on each side, arching upward near the margin and becoming loop-connected in the upper half of the lamina. Petioles 1–1.5 cm long, with same kind and density of pubescence as twigs. Inflorescences to 10 cm long, with same kind and density of pubescence as twigs, racemose, few-flowered (usually 2 flowers present on each inflorescence), bracts not present at anthesis. Pedicels to 6 mm long, appressed puberulous. Flowers yellow, 1.5–1.7 cm diam., fragrant (same odor as in some euglossine bee-pollinated flowers, fide collector). Tepals 6, subequal, the inner three narrower than the outer three, the inner surface with a dense, short pubescence. Stamens 9, 4-celled, the outer six with lateral cells, the inner three with extrorse cells, anthers glabrous, filaments not discernible in the glandular mass. Pistil 1.3 mm long, glabrous, the ovary partly sunken in the pubescent floral tube and covered by the glabrous glandular mass. Staminal glands strongly enlarged, fused, forming a thick wall outside the stamens. Fruit unknown. Flowers: January. Elevation range: below 100 m.

*Collection studied.* COLOMBIA. CHOCO: Río Mecana, *Juncosa 1675* (MO).

*Pleurothyrium grandiflorum* represents the extreme in the tendency toward large flowers and few-flowered inflorescences in the genus. Its venation type, with a rather weakly developed marginal vein, is not specialized and its pubescence type is also rather nondescript, quite unlike the brown-tomentose pubescence which is common in *Pleurothyrium*, but rarely found in the closely related *Ocotea* and *Nectandra*. *Pleurothyrium grandiflorum* is only known from the type collection in the Chocó, an area known to be rich in endemic species.

**Pleurothyrium hexaglandulosum** van der Werff, Ann. Missouri Bot. Gard. 75: 417. 1988. TYPE: Panama. Colón: Río Guanche, 5 km upstream from road to Portobelo, *Hammel & Trainer 14781* (holotype, MO; isotypes, BR, PMA). Figures 26, 27.

Small tree, to 5 m tall. Twigs terete, densely tomentellous, solid, diameter 5 cm below tip 5 mm. Leaves alternate, chartaceous, 30–45 × 10–15 cm, obovate, gradually narrowed toward the base, the base abruptly rounded to subcordate, the tip acuminate, the upper surface glabrous, the lower surface with some small appressed hairs, especially along midrib and lateral veins; lateral veins 14–18 on each side, immersed on upper surface, raised on lower surface, the veins arching toward the tip near the margin and prominently loop-connected in the upper two-thirds of the lamina. Petioles tomentellous, ca. 5 mm long, swollen, to 5 mm thick. Inflorescences in axils of cataphylls, to 65 cm long, brown puberulous, paniculate, the branchlets 3–4 times cymosely branched, the basal

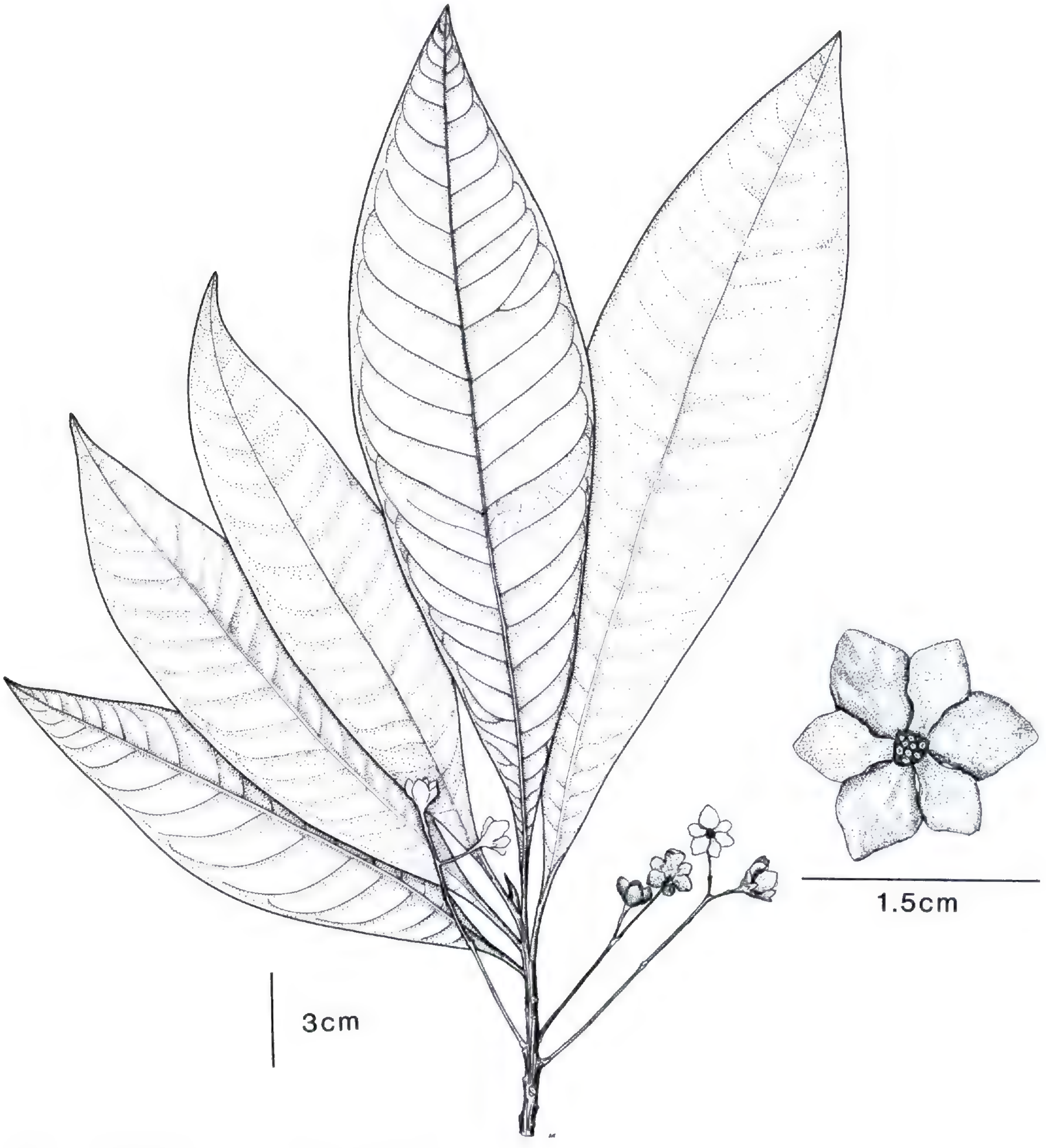



FIGURE 25. *P. grandiflorum*. Habit and flower.

branchlets to 25 cm long, the upper ones gradually shorter. Bracts absent at anthesis. Pedicels 1.5 (–2) cm long, densely gray-pubescent. Flowers ca. 10 mm diam., green, turning yellow. Tepals 6, equal, ca. 4 mm long, glabrous inside except where glands and stamens were not pressed against tepals, thus showing a narrow line of hairs in the center of the lower part of the tepal, this expended in a diamond-shaped pattern in the upper part; margin of tepals flat. Stamens 9, 4-celled, the outer six with introrse-lateral cells, the inner three with extrorse-lateral cells; in young flowers the anthers bent down and not raised above the glandular mass, but stamens becoming straight in older flowers with anthers clearly raised above the glands; filaments pubescent on the back. Glands conspicuously enlarged, but not fused, although enclosing the outer stamens. Ovary broadly ovoid, 1 × 1.5 mm, with short, gray pubescence, partly enclosed in the pubescent floral tube. Style ca. 0.5 mm long, with some gray pubescence. Glands and stamens deciduous in older flowers, leaving the ovary fully ex-

FIGURE 26. Distribution of *P. grandiflorum* (★), *P. hexaglandulosum* (●), *P. insigne* (○), and *P. intermedium* (■).

posed. Fruits unknown. Flowers: March. Elevation range: 150–200 m.

*Collections studied.* COSTA RICA. PUNTARENAS: Osa Peninsula, *Croat & Grayum 59792* (MO). PANAMA. COLON: Rio Guanche, ca. 5 km upstream from road to Portobelo, *Hammel & Trainer 14781* (BR, MO, PMA).

*Pleurothyrium hexaglandulosum* is only known from the type collection. The collection *Croat & Grayum 59792*, from the Osa Peninsula, Costa Rica, is tentatively placed here, although it differs in a number of minor characters. The twigs are almost glabrous, the inflorescences much shorter (to 15 cm long) and less pubescent, the tepals papillose, not pubescent, and the pedicels are shorter. On the other hand, the Costa Rican collection has the short, swollen petioles, the leaf shape, the pattern on the inner face of the tepals (though not as sharply outlined), and the androecial structure of the type of *P. hexaglandulosum*. Because the differences are quantitative and the leaf shape, thick petioles, and lax inflorescences are unmatched in *Pleurothyrium*, I place the Costa Rican collection in *P. hexaglandulosum*. However, if future collections show that the differences between the Panamanian and Costa Rican populations are consistent and not individual variation, it might be best to describe the Costa Rican material as a new taxon.

**Pleurothyrium insigne** van der Werff, sp. nov. TYPE: Ecuador. Napo: Reserva Biológica Jatun Sacha, tree, 12 m, tepals red outside, creamy-white inside, 13 Feb. 1987, *Palacios 1332* (holotype, MO; isotypes, AAU, C, COL, G, HBG, K, KUN, LE, NY, QAME, QRS, U). Figures 26, 28.

Arbor, ad 12 m alta. Ramuli teretes, solidi, ferrugineo-tomentosi, vetustiores glabrescentes. Folia alterna, firme chartacea, 20–60 × 7–15 cm, obovata vel anguste obovata, apice breviter acuminata vel rotundata, basi (acuta)

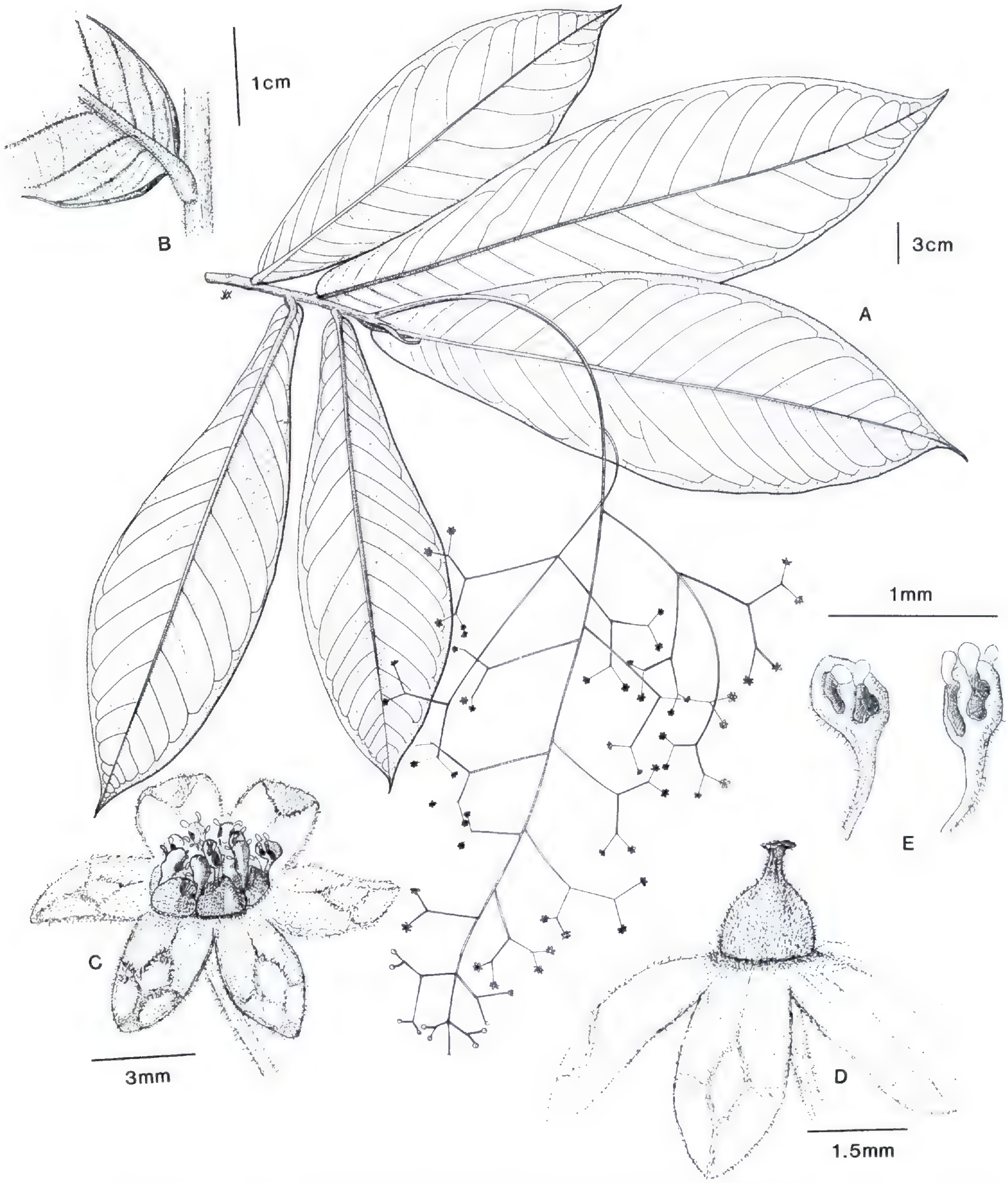



FIGURE 27. *P. hexaglandulosum.*—A. Habit.—B. Base of leaf.—C. Flower.—D. Old flower with androecium fallen off.—E. Stamens.

obtusa vel abrupte rotundata (cordata), supra praeter costae basem pubescentem glabra, subtus pilis erectis parvis praedita, indumento secus costam nervosque densiore castaneoque, venatione supra immersa, subtus costa nervisque elevatis; nervis (14–)18–26(–28) utroque costae latere, ad marginem in venam conspicuam marginalem terminantibus. Petioli 1.5–4 cm longi, ferrugineo-tomentosi. Inflorescentiae ad apices ramulorum ex axillis bractearum ortae, ferrugineo-tomentosae, ad 40 cm longae, paniculatae. Pedicelli ad 1 cm longi. Flores rotati, 12–15 mm diametro. Tepala 6, subaequalia, tres exteriora late elliptica, 5–6 × 4–5 mm, extus tomentella, intus minute papillosa; tres interiora 4–5 × 2.5 mm, extus basi tomentella, demum papillosa, intus papillosa. Stamina 9, 4-locellata, locellis lateralibus, glandulis permagnis, stamina cingentibus, staminodia parva, 3. Ovarium (depresse) globosum, ca. 1.5 mm diametro, basi glabrum, demum ferrugineo-tomentellum; stylo ca. 1 mm longo. Receptaculum intus tomentellum. Cupula verrucosa, 1.5 × 2.5 cm; fructus ellipsoideus, 2.5 × 2 cm.

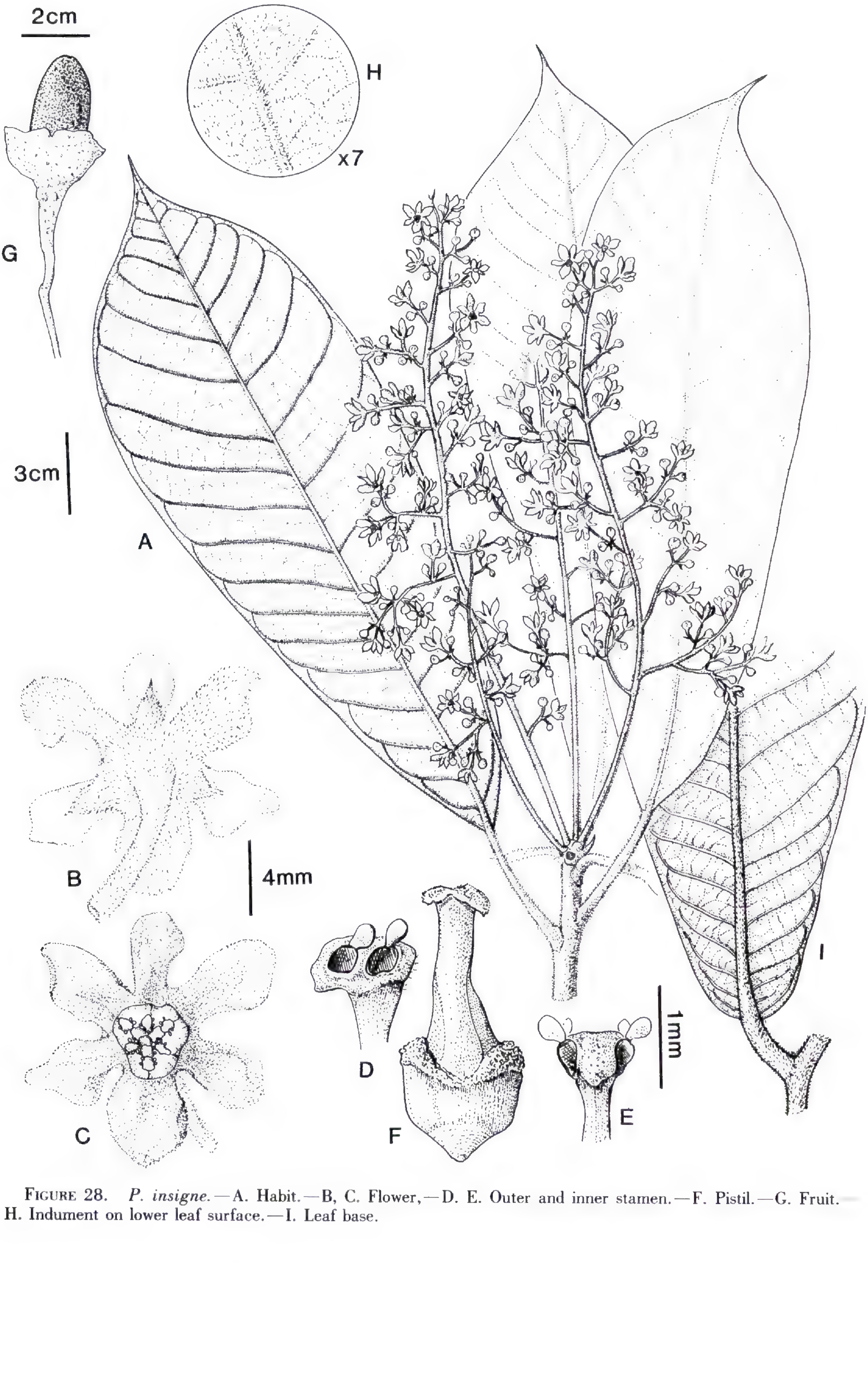



FIGURE 28. *P. insigne.*—A. Habit.—B, C. Flower,—D. E. Outer and inner stamen.—F. Pistil.—G. Fruit.—H. Indument on lower leaf surface.—I. Leaf base.

Small tree, to 12 m tall. Twigs solid, terete, 5–9 mm diam. 5 cm below the tip, ferruginous tomentose, but glabrescent with age. Leaves alternate, firmly chartaceous, 20–60 × 7–15 cm (narrowly) obovate, the base (acute) obtuse, abruptly rounded or cordate, the tip rounded or shortly acuminate; upper surface with some pubescence at the base of the midrib, otherwise glabrous, lower surface with an indument of erect hairs, this much denser on midrib and lateral veins; venation immersed on upper surface, midrib, lateral veins and marginal vein prominently raised on lower surface; lateral veins (14–)18–26(–28), connected by a conspicuous marginal vein. Petioles 1.5–4.0 cm long, to 5 mm diam., castaneous tomentose. Inflorescences clustered near tips of branches in axils of cataphylls, rarely along leafless short-shoots, 15–40 cm long, paniculate, ferruginous tomentose. Bracts of inflorescences, if present, to 4 mm long, ovate, tomentose outside, nearly glabrous inside. Pedicels to 1 cm long. Flowers reddish outside, greenish white inside, the tepals spreading, 12–15 mm diam. Tepals 6, subequal, outer 3 elliptic, 5–6 × 4–5 mm, tomentose outside, papillose inside, inner 3 elliptic, ca. 5 × 2.5–3 mm, outside with a basal, triangular, tomentose patch, otherwise papillose; inside papillose. Stamens 9, 4-celled, the cells lateral; staminodia 3, minute, linear, ca. 0.3 mm long, hidden by stamens and glands. Glands of inner stamens strongly enlarged and enclosing the outer stamens, forming a large mass, but not fully fused. Ovary (depressed) globose, ca. 1.5 mm diam., the base glabrous, upper part pubescent. Style ca. 1 mm long. Floral tube shallow, pubescent within. Cupule 1.5 × 3.5 cm or smaller, warty. Fruit ellipsoid, ca. 2.5 cm long, well exserted from cupule. Fruits: August–February. Flowers: June–November. Elevation range: 100–450 m.

*Collections studied.* BRAZIL. AMAZONAS: Humaita, near Tres Casas, *Krukoff 6232* (A, G, K, MO, NY, S, US). ECUADOR. MORONA-SANTIAGO: Pozo petrolero "Garza" de Tenneco, 35 km NE of Motalvo, *Zak 4511* (MO). NAPO: Jatun Sacha, 8 km downstream from Misahualli, *Palacios 1332* (AAU, C, COL, G, HBG, K, KUN, LE, MO, NY, QCNE, QRS, U, US); Jatun Sacha Biological Station, *Neill & Alvaredo 9033* (MO, QAME), *Palacios 1518* (MO), *Palacios 4388* (MO). PERU. LORETO: Varadero de Mazan, *Croat 19439* (MO, NY); Iquitos, Santa Maria del Ojeal on Río Amazonas, *Davidson 5336* (MO, NY); Maynas, Buena Suerte (Río Itaya), *Vásquez & Jaramillo 8444* (MO); Maynas, *Vásquez 9365* (MO); Requena, Sinchicuy, *Vásquez et al. 7823* (MO). PASCO: Oxapampa, Iscozacin, Arboretum, *Pariona 49* (MO). SAN MARTIN: San Martin, *Knapp & Mallet 8205* (MO).

*Pleurothyrium insigne* is a striking species, easily recognized by its large, obovate leaves with a pronounced marginal vein, the castaneous-tomentose indument of twigs, and the erect hairs on the lower leaf surface. Initially, I divided the specimens included in *P. insigne* between two species, one with abruptly rounded or cordate leaf base and short petioles (to 2 cm long), the other with an obtuse leaf base and longer (3–4 cm) petioles. Because some collections (for instance, *Krukoff 6232*) include specimens with obtuse and abruptly rounded leaf bases and the difference in petiole length is not consistent, I decided to place all specimens in one species, even though the extremes look quite different. The specimens with an abruptly rounded to cordate leaf base are very similar to *P. maximum*; the latter differs only in its glabrous lower leaf surface, smaller flowers, equal tepals, and relatively smaller glands. *Pleurothyrium maximum* is largely recognized because of the floral differences. I consider such differences as fundamental in *Pleurothyrium* and expect that additional collections of *P. maximum* will show that these differences will be consistent.

*Pleurothyrium insigne* is known from several widely scattered localities in Ecuador, Peru, and Brazil. The best collections are from the Jatun Sacha Biological Station, where the species is locally common. All collections from that area have leaves with an obtuse base; Peruvian collections and the sole Brazilian collection can have obtuse or abruptly rounded/cordate leaf bases.

**Pleurothyrium intermedium** (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra intermedia* Mez, Repert. Spec. Nov. Regni Veg. 16: 308. 1920. TYPE: Brazil. Acre: Seringal São Francisco, *Ule 9408* (holotype, B; isotype, K). Figure 26.

Tree or shrub, 5–20 m tall. Twigs terete, solid, sparsely pubescent to glabrous, diameter 5 cm below the apex ca. 3 mm. Terminal buds densely appressed yellowish pubescent, the bud contrasting with the dark twig. Leaves alternate, chartaceous, elliptic to obovate-elliptic, 9–16 × 3–5 cm, the base acute, the tip obtuse, upper surface glabrous, the venation immersed, the lower surface glabrous or nearly so, the midrib raised, lateral veins weakly raised; lateral veins 10–12 on each side, arching upward near the margin, not or very weakly connected with the superior vein. Petioles ca. 1.5 cm long, with similar tomentum as twigs. Inflorescences in axils of deciduous bracts, ca. 12 cm long, paniculate, the branchlets with racemosely arranged cymes, often the two lateral flowers of a cyme missing; main axis sparsely pubescent, the

FIGURE 29. *P. marginale.*—A. Habit.—B. Flower.—C. Base of leaf underside, showing indument.

branchlets denser pubescent, pedicels almost white pubescent, 2–3(–5) mm long. Flowers yellowish green, ca. 3 mm diam., the tepals ± erect at anthesis. Tepals 6, equal, ovate, ca. 2 mm long, puberulous outside, papillose inside, the margin reflexed. Stamens 9, 4-celled, the cells lateral, filaments glabrous, about as long as the anthers, glands enlarged, but not fused and not surrounding the outer stamens, but visible as large lobes separating the outer stamens; anthers raised above the level of the glands. Ovary glabrous, ovoid, gradually narrowed into the short style, stigma platelike; pistil 1.8 mm long. Floral tube glabrous inside. Fruit unknown. Flowers: August. Elevation range: 100–200 m.

*Collections studied.* BOLIVIA. SANTA CRUZ: Ichilo, Reserva Forestal Chore, Camp. Arroyo Perdido, *Neill 9435* (MO, QCNE), *Neill 9439* (MO, QCNE). BRAZIL. AMAZONAS: Seringal São Francisco, *Ule 9408* (B, K). PERU. MADRE DE DIOS: Tambopata, Hermosa Chica, *Pesha 10* (MO).

*Pleurothyrium intermedium* is only known from the type collection, two recent collections from Bolivia, and one recent collection from Peru. It belongs to the group of species with erect tepals at anthesis and is most closely related to two other, equally poorly known, species from Brazil (*P. amplifolium* and *P. undulatum*). More collections are needed for a better understanding of the status of those three species.

**Pleurothyrium marginale** van der Werff, sp. nov. TYPE: Colombia. Valle: Río Cajambre near Barco on the Pacific coast, elev. 5 80 m, *Cuatrecasas 17196* (holotype, US; isotype, F). Figures 29, 30.

FIGURE 30. Distribution of *P. marginale* (★), *P. maximum* (●), *P. nobile* (○), and *P. obovatum* (■).

Arbor, ad 20 m. Ramuli teretes, solidi, minute fusco-puberuli, glabrescentes. Folia alterna, firme chartacea, elliptica, 8–14 × 3–5 cm, basi acuta vel attenuata, apice acuminata, supra glabra vel paucis pilis adpressis munita, subtus sparse adpresse strigosa, indumento densiore secus costam nervosque laterales; nervis lateralibus 8–12 utroque costae latere. Venatio brochidodroma, supra immersa, subtus costa, nervis lateralibus et venatione tertia elevata. Petioli 15–22 mm longi. Inflorescentiae ex axillis bractearum ortae, fusco-tomentulosae, 4–6 cm longae, racemosae, uni- vel biflorae, bracteis sub anthesi absentibus. Pedicelli ca. 4 mm longi, pedunculi ca. 9 mm longi, fusco-tomentulosi. Tepala 6, subaequalia, 3 exteriora late ovata, ca. 5 mm longa, 3 interiora rhomboidea, basi late et breviter stipitata, ca. 4 mm longa, in sicco utrinque fusco-tomentella. Stamina 9, 4-locellata, locellis lateralibus, antheris glabris, glandulis incrassatis, coalitis, stamina cingentibus. Ovarium ellipsoideum, glabrum, ca. 0.8 mm longum; stylum glabrum, ca. 1 mm longum, stigma peltatum. Tubus floralis glaber. Fructus perjuvenalis in tubo florale inclusus; fructus adultus ignotus.

Tree, 20 m tall. Twigs terete, solid, minutely brown-puberulous, glabrescent, ca. 3 mm diam. 5 cm below the tip. Leaves alternate, not clustered, firmly chartaceous, elliptic, 8–14 × 3–5 cm, the base acute to attenuate, the tip acuminate, the upper surface glabrous or with some minute hairs, especially near the base of the midrib, the lower surface with scattered, minute, appressed hairs, these denser along midrib and lateral veins; venation brochidodromous, immersed on upper surface, midrib and lateral veins raised on lower surface, a marginal vein well developed; lateral veins 8–12 on each side. Petioles 15–22 mm long, flattened on upper surface, pubescence similar to that of twigs. Inflorescences in axils of cataphylls, brown-tomentulose, 4–6 cm long, racemose, 1–2-flowered (but probably several flowers fallen off), bracts absent at anthesis. Flowers yellow fide collector, ca. 12 mm diam. Pedicel ca. 4 mm long, peduncle ca. 9 mm long, brown-tomentulose. Tepals 6, subequal, the outer three broadly ovate, ca. 5 mm long, the inner three mostly rhombic with a short, broad stalk, ca. 4 mm long; both inside and outside brown tomentellous in sicco. Stamens 9, 4-celled, the cells lateral, opening back-to-back, anthers glabrous; glands enlarged, fused, enclosing the stamens. Ovary ellipsoid, ca. 0.8 mm long, glabrous, style glabrous, ca. 1 mm long, stigma platelike. Floral tube

glabrous inside. Very young fruit fully enclosed in the enlarged floral tube; mature fruit unknown. Flowers: April. Elevation range: below 100 m.

*Collection studied.* COLOMBIA. VALLE: Costa del Pacifico, Río Cajambre, *Cuatrecasas 17196* (F, US).

A species only known from the type collection, *Pleurothyrium marginale* derives its name from its well-developed marginal vein. This species can be readily identified also by the sparse, appressed indument on the lower leaf surface and the few-flowered inflorescences. The collector indicated that the tree had tall buttresses (as in *Cecropia*) and canary-yellow wood. Buttresses are rare among neotropical Lauraceae: I have only seen them in a *Caryodaphnopsis* species from Peru. Yellow wood is a common feature in *Aniba*, but is infrequent outside this genus. The wood is used for making boards and canoes; the common name is palo blanco.

**Pleurothyrium maximum** O. C. Schmidt, Notizbl. Bot. Gart. Berlin-Dahlem 10: 235. 1928. *Ocotea maxima* (O. C. Schmidt) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Peru. Amazonas: mouth of Río Santiago, Pongo de Manseriche, terra firma forest, 160 m elev., *Tessman 4040* (holotype, B; isotypes, G, NY). Figure 30.

Small tree, 4–6 m tall. Twigs terete, solid, ferruginous tomentose, glabrescent in age, 5–6 mm diam. a few cm below the tip. Leaves alternate, chartaceous or firmly chartaceous, 30–50 × 7–15 cm, obovate to narrowly obovate, gradually narrowed toward the base, the base abruptly rounded to cordate, the tip acute to acuminate, glabrous above, the lower surface with a few scattered, minute, appressed hairs, otherwise glabrous; midrib and lateral veins immersed on upper surface, prominently raised on lower surface, the tertiary venation weakly raised. Lateral veins 20–30 on each side, near the margin connected by a conspicuous marginal vein. Petioles 1–2 cm long, 4–5 mm diam., with similar pubescence as the twigs. Inflorescences slender, lax, 40–65 cm long, ferruginous tomentose, the branchlets once or twice cymosely branched, in axils of cataphylls at tips of twigs, bracts mostly lacking at anthesis. Pedicels 5–9 mm long, ferruginous tomentose. Flowers rotate, ca. 8–9 mm diam. dark green-red-brown outside, dark green inside, the glands bright green, stamens yellowish. Tepals 6, equal in shape and size, 2.5 × 1.5 mm, the margin flat, the outer three ferruginous tomentellous outside, the inner three with a basal, triangular, tomentellous patch, otherwise glabrous; all tepals glabrous inside except for a narrow line of short hairs in the center of the lower part, this expanded into a diamond-shaped outline in the upper part. Stamens 9, 4-celled, the outer six with 2 cells lateral and 2 cells introrse, the inner three with one pair lateral and one extrorse; glands enlarged, protruding between and ± enclosing the outer stamens, but definitely free. Immature ovary globose to ovoid, 1–1.5 mm long, covered with short brown hairs; style glabrous. Floral tube inside covered with short reddish hairs. Fruit and cupule unknown. Flowers: September–November. Elevation range: below 200 m.

*Collections studied.* PERU. AMAZONAS: mouth of Río Santiago, Pongo de Manseriche, *Tessmann 4040* (B, G, NY), *Tessmann 4529* (B, G, NY).

*Pleurothyrium maximum* is only known from two collections from the area where the Río Santiago joins the Río Marañon, in northern Peru. It is vegetatively similar to *P. insigne*, which see for further discussion. *Pleurothyrium maximum* also resembles *P. williamsii*, which differs in its narrower leaves (5 cm above the base, 2–3.5 cm wide vs. 5–6 cm wide), shorter indument on twigs (or glabrous) and inflorescences, thinner leaves that dry dark green, and shorter inflorescences (but few inflorescences are known). In *P. maximum* the glands of the stamens are free and do not form a wall surrounding the stamens, while in *P. williamsii* the glands do form a wall, with only a faint line indicating the boundaries of the individual glands.

**Pleurothyrium nobile** A. C. Smith, Phytologia 1: 120. 1935. *Ocotea nobilis* (A. C. Smith) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Brazil. Amazonas: near mouth of Rio Embira, *Krukoff 5121* (holotype, NY not seen; isotypes, A, B, G, K, MO, S, US). Figure 30.

Tree, 25 m tall. Twigs solid, terete or ridged, glabrous, 6–7 mm diam. 5 cm below the apex. Terminal bud brown-tomentellous. Leaves alternate, stiffly chartaceous, elliptic, 15–30 × 6–12 cm, the base obtuse to rounded, the tip acute, glabrous on both surfaces, venation immersed on upper surface, midrib and lateral veins raised on lower surface, tertiary venation weakly raised on lower surface, lateral veins 7–10 on each side, arching upward near the margin, but not or very weakly connected with the superior vein. Petioles 2–3 cm long, glabrous, canaliculate. Inflorescences in axils of cataphylls, to 12 cm long, minutely

puberulous, glabrescent, paniculate, the branchlets 3–4 times cymosely branched, few-flowered, bracts not present at anthesis. Pedicels 3–4 mm long. Flowers ca. 10 mm diam. Tepals 6, equal, brown-puberulous on outside, minutely brown-papillose to glabrous inside, ovate, ca. 4 mm long. Stamens 9, 4-celled, the cells lateral, anthers and upper part of filaments brown-papillose, glands large, completely surrounding the stamens but not fully fused. Ovary ovoid, ca. 2 mm long, the lower part glabrous, the upper part brown-papillose, except for six large glabrous spots, where glands were in contact with ovary; style poorly differentiated, brown-papillose, 0.2 mm long. Floral tube glabrous inside. Cupule and fruits unknown. Flowers: June–July. Elevation range: 200–300 m.

*Collections studied.* BRAZIL. AMAZONAS: mouth of Rio Embira, *Krukoff 5121* (A, B, G, K, MO, NY, S, US). PERU. HUANUCO: Puerto Inca, Dtto. Llullapichis, *Kroll 285* (MO), *Kroll 422* (MO). LORETO: Coronel Portillo, Km 98 carretera Pucallpa–Huanuco, *M. Castillo 12* (F, K, MO, NY, US, WIS), *M. Castillo 15* (F, K, US).

*Pleurothyrium nobile* is rarely collected and is known only from five collections. The type collection was made in varzea forest, two later collections (both from the same tree) in dry tropical forest, and two from wet forest. The recent collections have smaller, less-branched inflorescences, but the collections agree well in leaf shape, type of indumentum, and floral characteristics. Smith (1935) cited *Krukoff 4800* as a paratype of *P. nobile*. Because this collection has a whitish, very short appressed indument on lower leaf surface, acuminate leaf tips, and slender inflorescences, I include it in *P. panurense* (Meissner) Mez. The common name for the species in Peru is *lobo moena*.

**Pleurothyrium obovatum** van der Werff, sp. nov. TYPE: Ecuador. El Oro: 15 km NW of Paccha on the road to Pasaje, 1,800 m elev., *Brandbyge 42366* (holotype, AAU). Figures 30, 31.

Arbor parva, ad 10 m alta. Ramuli teretes, fistulosi. Gemma terminalis ferrugineo-tomentella. Folia alterna, perobovata, 40–45 × 16–20 cm, firme chartacea, basi acuta, apice rotundata vel breviter acuminata, glabra. Nervi laterales ca. 20 utroque costae latere, venatione leviter brochidodroma. Inflorescentiae ex axillis bracteārum ortae, interdum fistulosae, ferrugineo-tomentelli, 20–30 cm longae, paniculatae. Flores ca. 11 mm diametro. Tepala 6, aequalia, elliptica, dense tomentella vel papillosa. Stamina 9, 4-locellata, locellis interioribus extrorsis, superioribus lateralibus, antheris erectis, super glandulas prominentibus. Glandulae liberae. Ovarium ellipsoideum, glabrum, stylo ca. 1 mm longo, papillis ferrugineis praedito. Tubus floralis glaber. Fructus ignoti.

Small tree, to 10 m tall. Twigs terete, fistulose, with scattered small, erect ferruginous hairs, diameter of twigs 5 cm below tip ca. 9 mm. Terminal bud minutely, but densely, ferruginous tomentellous. Leaves alternate, strongly obovate, 40–45 × 16–20 cm, firmly chartaceous, gradually narrowed to the acute base, the tip blunt or with a very short acumen, glabrous on both surfaces, midrib slightly raised or immersed, otherwise venation immersed on upper surface, midrib prominently raised on lower surface, lateral veins and tertiary venation progressively less raised. Lateral veins ca. 20 on each side, near the margin arching upward and in the distal half of the lamina connected with the superior vein, but a marginal vein not well developed. Petioles ca. 2 cm long, glabrous or with some scattered ferruginous hairs, 5 mm diam. Inflorescences in axils of cataphylls, sometimes fistulose, ferruginous-tomentellous, 20–30 cm long, paniculate, the lateral branches 2–3 times cymosely branched, many-flowered, bracts deciduous at anthesis. Pedicels ca. 3 mm long, gradually widened in floral tube. Flowers outside ferruginous brown, inside whitish, ca. 11 mm diam., rotate. Tepals 6, equal, 4 mm long, elliptic, densely tomentellous or papillose on both surfaces, the margins plane. Stamens 9, 4-celled, the lower pair extrorse, the upper pair lateral, the cells large; anthers erect and raised well above the glands. Glands not completely enclosing the outer stamens, not fused. Ovary ellipsoid, ca. 1.5 mm long, glabrous, gradually narrowed into the style, this ca. 1 mm long and with some ferruginous papillae; stigma platelike. Floral tube glabrous inside. Very young fruit fully enclosed in floral tube. Fruits and cupules unknown. Flowers: September. Elevation range: 1,000–1,800 m.

*Collections studied.* ECUADOR. AZUAY: Cuenca, El Sillado, Parque Molleturo, *Ortiz-Proyecto Molleturo 192* (MO). EL ORO: Pasaje, 15 km NW of Paccha on road to Pasaje, *Brandbyge 42366* (AAU). LOJA: 15 km E of Alamor on road to Celica, *Brandbyge 42343* (AAU).

*Pleurothyrium obovatum* is only known from three recent collections in southern Ecuador. The fistulose (lenticellate?) branches, relatively small glands of the stamens, and floral shape indicate a close relationship to the *P. cuneifolium* group. *Pleurothyrium obovatum* is, however, easily recognized by the ferruginous indument, which becomes floccose on older twigs, and obovate, glabrous leaves. The large, erect anthers are another character of this species. The leaves of the two Brandbyge collections are more narrowed toward the base than the Ortiz collection, and it is likely

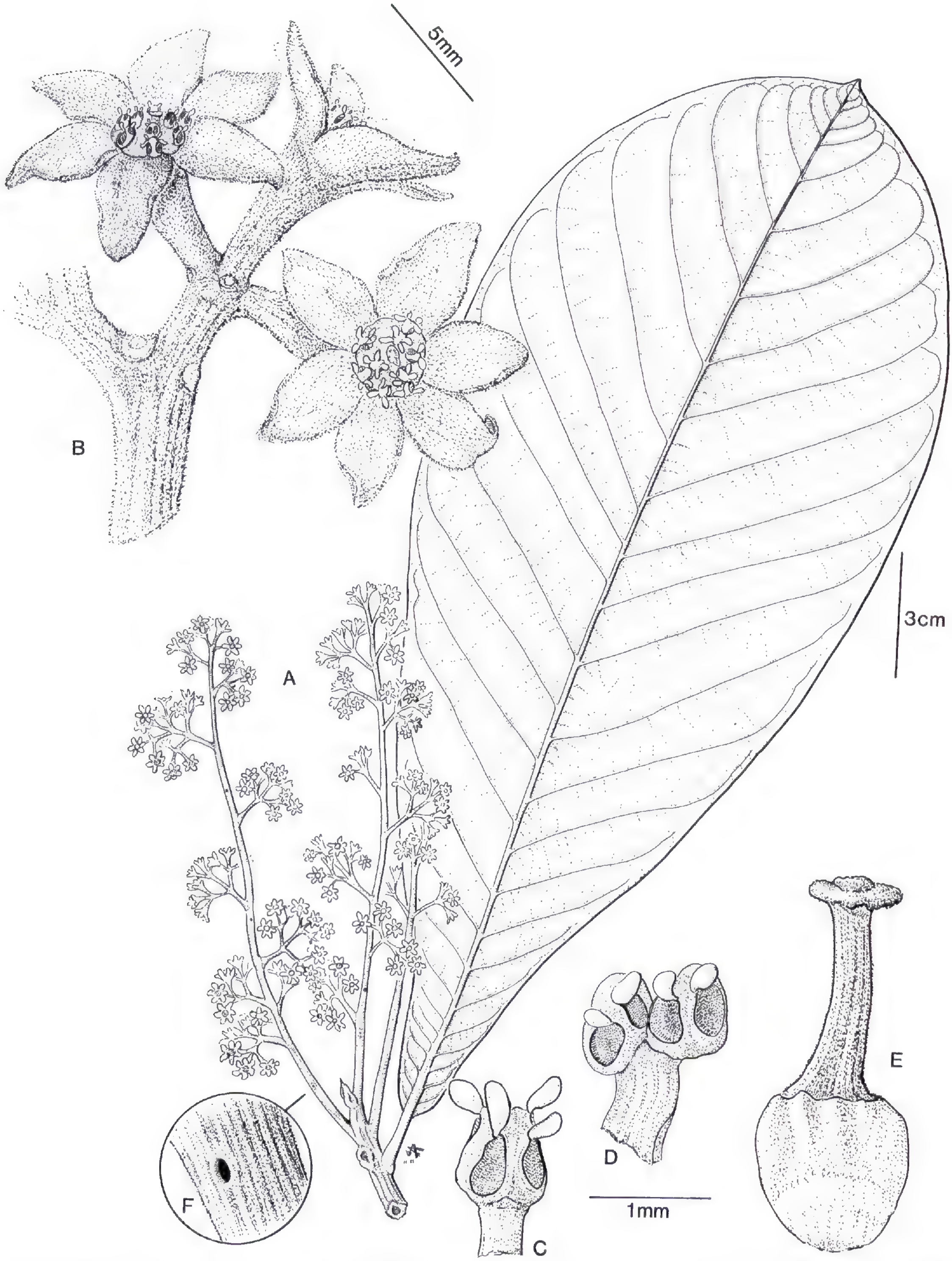



FIGURE 31. *P. obovatum.*—A, Habit.—B. Flowers.—C. Stamen (Whorl I).—D. Stamens (Whorls I and III) with fused filaments.—E. Pistil.—F. Detail of inflorescence axis, showing hole used as passage by ants.

FIGURE 32. Distribution of *P. palmanum* (★), *P. panurense* (●), and *P. prancei* (○).

that the few collections do not show the full range of morphological variation.

**Pleurothyrium palmanum** (Mez & J. D. Smith) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 41. 1986. *Ocotea palmana* Mez & J. D. Smith, Bot. Gaz. (Crawfordsville) 33: 258. 1902. TYPE: Costa Rica. San José: La Palma, *Tonduz CR 12652 = J. D. Smith Herb. 7374* (B, GH, US: also reported in K, M; holotype not designated). Figure 32.

Trees, to 20 m tall. Twigs solid, ridged or terete, tomentulose with brown or yellow-brown hairs. Terminal bud tomentulose. Leaves alternate, clustered near the tips of branches, chartaceous, 15–28 × 7–15 cm, obovate or broadly obovate, the base cuneate or acute, the tip rounded or with a very short, blunt acumen, upper surface with short, brown pubescence along midrib, otherwise glabrous, lower surface densely yellow-brown to brown-tomentulose, sometimes with taller hairs mixed in, lateral veins 5–9 on each side, these arching toward the tip and becoming weakly loop-connected in the distal half of the lamina; venation immersed on the upper surface or the midrib slightly raised, midrib and lateral veins elevated on lower surface, tertiary venation slightly raised. Petioles 1–2 cm long, terete, with similar pubescence as twigs. Inflorescences in axils of cataphylls, 4–10 cm long, paniculate, the branchlets once cymosely branched, rarely depauperate and racemose, with up to 20 flowers, brown-tomentellous, bracts subtending flowers sometimes persisting, these elliptic, to 4 mm long, tomentellous on both surfaces. Pedicels ca. 3 mm long, tomentellous. Flowers ca. 10–12 mm diam. Tepals 6, equal in size, ca. 5 mm long, elliptic, the outer three tomentellous outside, inner three papillose except for the tomentellous base; all tepals papillose inside. Stamens 9, 4-celled, the cells lateral, the valves nearly back-to-back; filaments and anthers each ca. 1 mm long, papillose; glands large, partially fused, but not enclosing all outer stamens. Style ca. 1.5 mm long, papillose;

ovary globose, glabrous, ca. 1 mm long, enclosed in the glabrous floral tube. Cupule and fruit unknown. Flowers: November. Elevation range: 1,000–1,600 m.

*Collections studied.* COSTA RICA. LA PALMA: *Rowlee 233* (F, US), CARTAGO: *Barbour 1011* (F, MO). PUNTARENAS: Reserva Biológica Monteverde, Powell Trail, Pacific slope, *Haber 9526* (MO). SAN JOSE: La Palma, *Tonduz 12652* (B, GH, US). PANAMA. CHIRIQUI: Palo Alto, just E of Boquete, *Stern et al. 1064* (MO).

*Pleurothyrium palmanum* is a rarely collected species. The concept of this species accepted here is different from that in Burger & van der Werff (1990); one of the two flowering collections cited in that publication (*Barbour 1012*) is here excluded from *P. palmanum*. It differs in its indument (lower leaf surface is nearly glabrous, not entirely covered by a brown-tomentellous indument) and flower structure (glands are fused and enclosing stamens, not only partly fused and not enclosing stamens). The only flowering collections I have seen are the type and *Haber 9526*. The glands in *P. palmanum* are not strongly enlarged and the stamens are erect, with the lower pair of locelli lateral and the upper introrse. The available collections are quite variable in leaf size. The type has large (18–28-cm-long) leaves; *Barbour 1011*, a sterile collection, has leaves to 15 cm long, while *Stern et al. 1064* (from Chiriquí, Panama) and *Haber 9526* have even smaller leaves, to 10 cm long. Because *Haber 9526* and the type have the same flower type, leaf shape (± obovate), and indument, I attach no taxonomic value to the striking variation in leaf size. The collection *Barbour 1012* remains unplaced. As mentioned earlier, I exclude it from *P. palmanum*, but the specimens (a MO and a US sheet) have few flowers, some of which had been dissected by earlier botanists and were unrecognizable, while others were covered with fungus or were otherwise damaged. Vegetatively, *Barbour 1012* somewhat resembles *P. golfodulcense*.

**Pleurothyrium panurense** (Meissner) Mez, Jahrb. Bot. Gart. Berlin 5: 468. 1889. *Nectandra panurensis* Meissner, D.C. Prodr. 15(1): 157. 1864. *Ocotea panurensis* (Meissner) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Brazil. Amazonas: near Panure along the Rio Uaupés, *Spruce 2449* (B, BM, BR, E, G, K; holotype not designated). Figures 32, 33.

Tree, to 20 m tall. Twigs solid, terete, minutely brown-tomentellous, ca. 4 mm diam. 5 cm below the apex. Terminal bud brown-tomentellous. Leaves clustered near tips of branches, chartaceous, 15–30 × 6–10 cm, elliptic to elliptic-obovate, the base obtuse or rounded, the tip acuminate; upper surface glabrous, lower surface covered with a very fine, almost appressed whitish tomentum, this partially wearing off on older leaves; lateral veins 12–16, arching upward near the margin and loop-connected in the upper half of the laminae, venation immersed on upper surface, costa and lateral veins raised on lower surface. Petioles 5–14(–24) mm long, with similar indument as twigs. Inflorescences in the axils of cataphylls, brown-tomentellous, 5–10 cm long, paniculate, the branchlets 1–2 times cymosely branched, 15–30-flowered, bracts deciduous at anthesis. Pedicels to 5 mm long. Flowers white, ca. 8 mm diam. Tepals 6, equal, outer three gray-tomentellous outside, inner three with a basal triangular tomentellous patch, otherwise glabrous, elliptic, ca. 3 mm long. Stamens 9, 4-celled, all with 2 cells extrorse, the other pair lateral; stamens scarcely raised above the glandular mass that completely surrounds the stamens; ovary glabrous, globose, ca. 1.3 mm long, enclosed mostly in the rather deep, glabrous floral tube, the upper part covered by the glands; style ca. 0.5 mm long, papillose; stigma platelike. Cupule deeply cup-shaped, 2–2.5 cm wide, ca. 1.5 cm long, warty, gradually narrowing into the pedicel. Fruit ellipsoid, ca. 2.3 cm long, 1.4 cm wide. Fruits: December–April. Flowers: May–June. Elevation range: 100–200 m.

*Collections studied.* BRAZIL. AMAZONAS: near mouth of Rio Embira, *Krukoff 4783* (G, NY); mouth of Rio Embira, tributary of River Tarauaca, *Krukoff 4800* (A, F, G, MO, NY); Rio Apitua tributary of Rio Purus, 120 km S of Labrea, *Prance 13927* (NY); Panure ad Rio Uaupes, *Spruce 2449* (B, BM, BR, E, G, K). PERU. LORETO: Maynas, Mishana, Río Nanay, *Ayala 5734* (MO); Maynas, vicinity of Iquitos, *Revilla 3687* (MO); Maynas, Pto. Almendras, *Vásquez 10233* (MO); San Antonio, Río Pintuyacu, *Vásquez et al. 7468* (MO). UCAYALI: Coronel Portillo, Leoncio Prado (Yarina Cocha), *Vásquez 4970* (MO).

*Pleurothyrium panurense* is a rarely collected species, known with certainty from six collections: the type collection, four recent collections from Peru, and a collection from Brazil. All collections, including the type (indicated on the K sheet), come from inundated forest. Allen (1964) listed two additional collections of *P. panurense*, *Froes 20526* and *21295* (both NY), and presented a description of cupule and fruit based on *Froes 20526*. I assign these collections to *P. vasquezii* because the pubescence on the lower leaf surface consists of scattered, erect hairs (not a finely appressed, whitish indument) and because the leaves are not clustered.

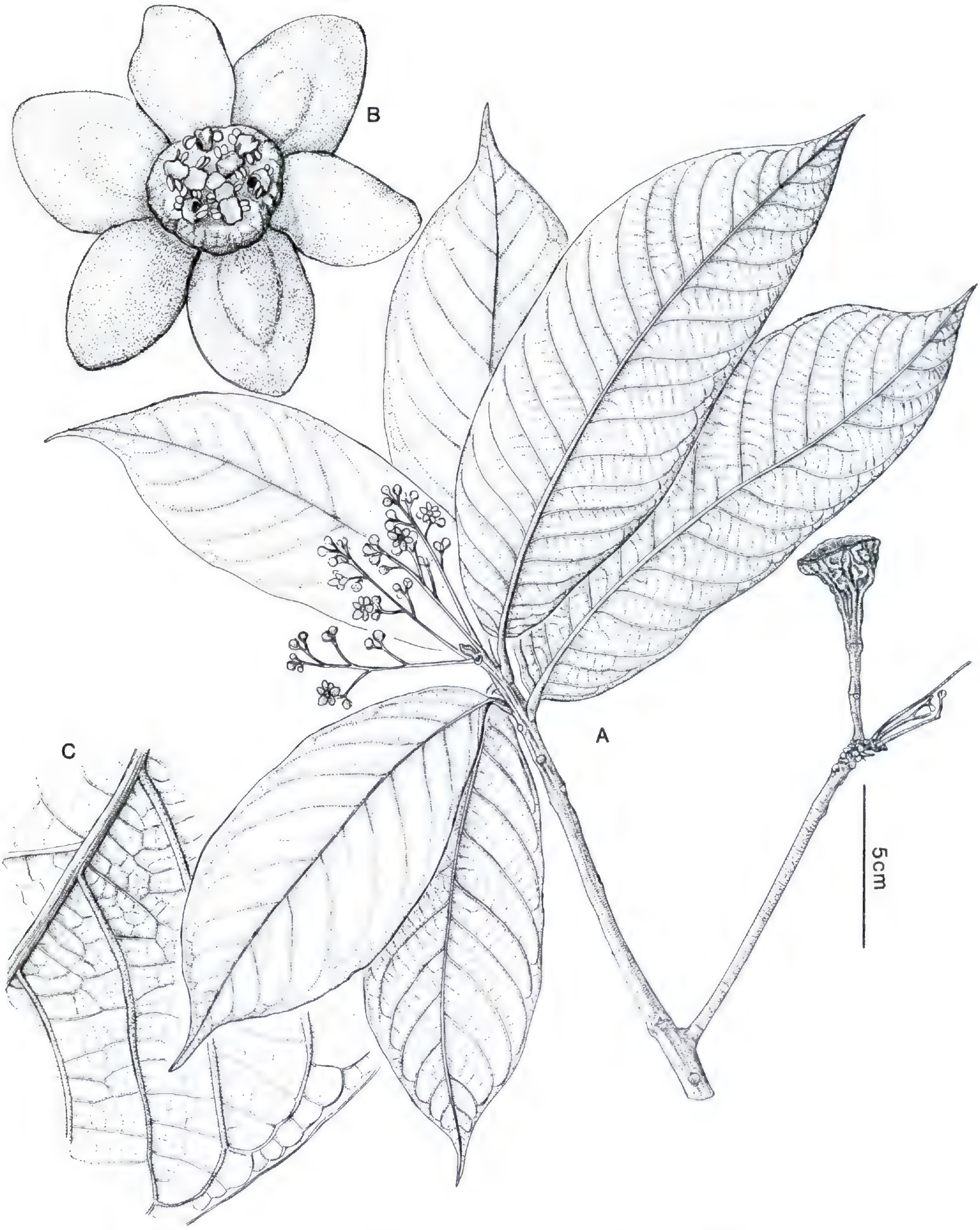



FIGURE 33. *P. panurense*.—A. Habit.—B. Flower.—C. Detail of lower leaf surface.

Also, the marginal vein is more strongly developed, and the pubescence on the young twigs is ferruginous-tomentose rather than light-brown tomentellous. Thus, Allen's description of cupules and fruits of *P. panurense* should be ignored.

Actually, *Pleurothyrium panurense* can be readily identified by the following combination of characters: short (to 10-cm-long) inflorescences, inner face of tepals glabrous, leaves clustered, leaves with an obtuse or rounded base, and leaves with a whitish indument on lower leaf surface. The flower size is normal for the genus and the glands are well developed.

It is likely that *Prance et al. 13927* (NY) be-

FIGURE 34. Distribution of *P. parviflorum* (★), *P. pauciflorum* (●), and *P. pilosum* (○).

longs here, too. However, the leaves are rather narrow and not clustered; the indument agrees with *Pleurothyrium panurense*. Unfortunately, the specimen is sterile.

*Krukoff 4800* and *Vasquez 4970* are provisionally placed here. They differ from *P. panurense* in their acute leaf bases and longer petioles (18–24 mm vs. 5–13 mm in typical *P. panurense*), but agree well in inflorescence and floral characters. Both collections were made in flooded forest. Although it is possible that future collections will show these collections to be different from *P. panurense*, I prefer to include them for the time being in *P. panurense*. *Krukoff 4800* was cited by A. C. Smith as a paratype of *P. nobile*, but it differs from that species in its indument.

**Pleurothyrium parviflorum** Ducke, Arch. Jard. Bot. Rio de Janeiro 5: 114. 1930. *Ocotea parviflora* (Ducke) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Brazil. Amazonas: Igarapé do Lago de Serpa prope Itacoatiara, ad ripas inundatas, *Ducke RB 19935* (holotype, RB; isotypes, B, U). Figures 34, 35.

*Pleurothyrium densiflorum* A. C. Smith, Bull. Torrey Bot. Club 58: 109. 1931. *Ocotea compactiflora* Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Peru. Loreto: Mishuyacu, *Klug 1372* (holotype, NY not seen; isotype, US).

Tree, to 30 m tall, but usually not exceeding 20 m. Twigs slightly angular or terete, fistulose, glabrous or nearly so, ca. 5 mm diam. a few cm below the tip. Terminal bud covered with gray, fine appressed hairs. Leaves alternate, chartaceous, 10–20 × 3.5–9 cm, elliptic, the base acute to truncate, apex acute, glabrous or nearly so on both surfaces. Lateral veins 10–15 on each side, curving toward the tip near the margin, but not uniting with the superior veins; veins immersed on upper surface, midrib and lateral veins raised on lower surface. Petioles 10–15 mm long, glabrous, somewhat canaliculate. Inflorescences in axils of leaves or cataphylls, glabrous or with some minute appressed pubescence, 5–15 cm long, the branches up to 4 times cymosely branched, frequently flat-

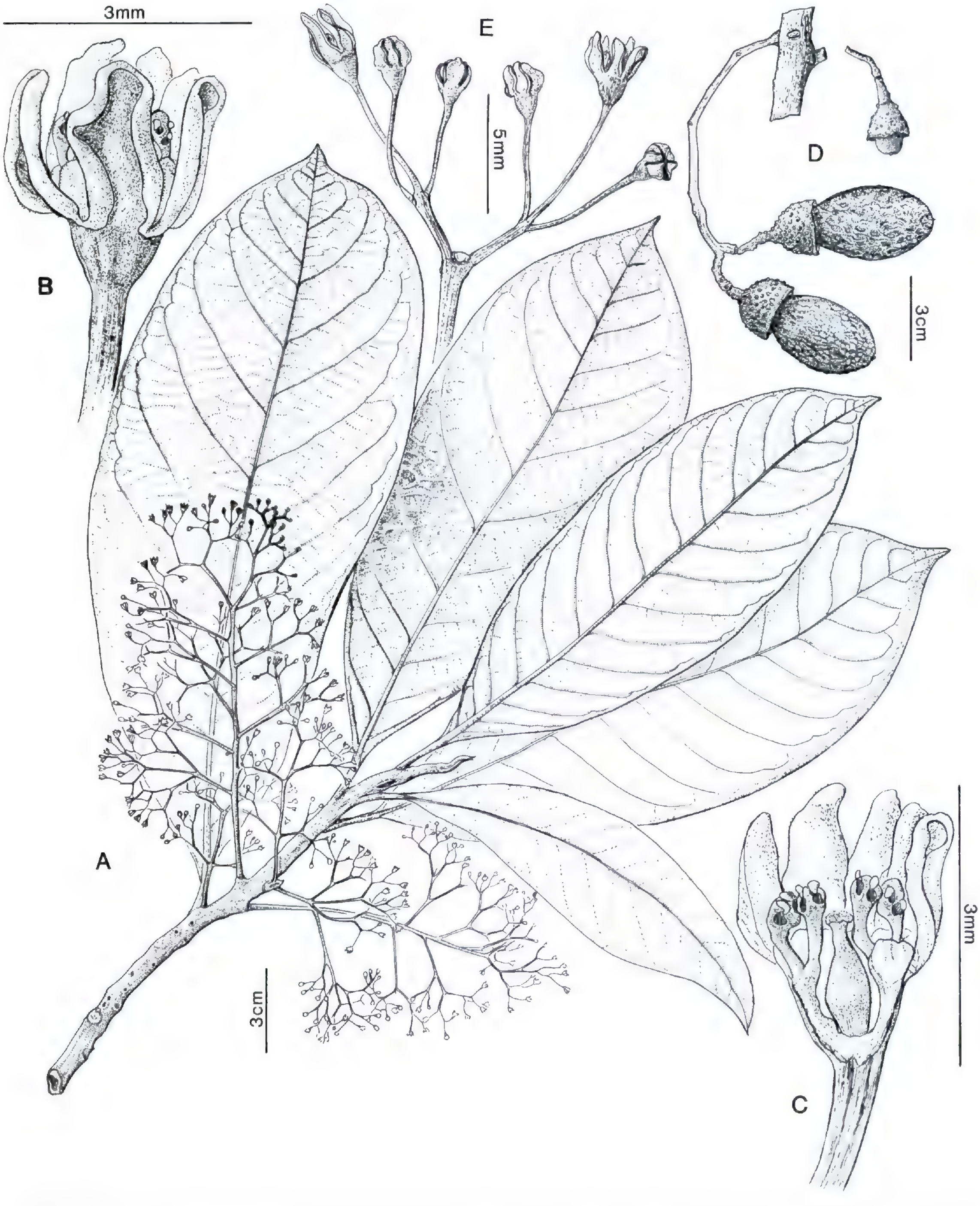



FIGURE 35. *P. parviflorum.*—A. Habit.—B. Flower.—C. Cross section of flowers.—D. Fruit.—E. Part of inflorescence.

tened, many-flowered; bracts absent at anthesis, but present in younger parts of inflorescences, linear, to 2.5 mm long, glabrous or with some minute appressed pubescence, the margin ciliate. Pedicels 3–5(–7) mm long. Flowers green or greenish white, ca. 5 mm diam. Tepals 6, equal, narrowly elliptic, ca. 2 mm long, the margins reflexed, glabrous or minutely papillose outside, papillose on inner surface. Stamens 9, ca. 0.9 mm long, 4-celled, the cells lateral, filaments glabrous, as long as anthers. Glands almost completely encircling the outer stamens, but not fused. Ovary glabrous, ellipsoid, ca. 0.7 mm long, gradually narrowed into the 0.4-mm-long, glabrous style. Floral tube deep, fully en-

closing the ovary, glabrous. Cupule with large lenticels, completely enclosing the fruit when young, at maturity bowl-shaped, 2.5 cm wide, 1 cm high, sometimes smaller and shallower; fruit ellipsoid, 3.6 × 2.7 cm, well exserted. Fruits: December–April. Flowers: April–August. Elevation range: 100–300 m.

*Collections studied.* BRAZIL. ACRE: Rio Moa, 10 km from Maita, *Prance et al. 11970* (K, NY). AMAZONAS: Itacoatiara, Igarape de Serpa, *Ducke RB 19935* (B, RB, U); Rio Jutahy, *Froes 21036* (F, NY); Rio Asapinus, Tapajos, *Miranda Bastos 17* (RB); delta of Rio Jauaperi, *Mori 20470* (MO, NY); mouth of Rio Ica along Rio Solimões, *Mori et al. 9074* (K, MO, NY); Mun. Jutai, Est. Ecologica Jutai-Solimões, *Cid Ferreira et al. 7292* (MO, NY). ECUADOR. NAPO: Río Cuyabeno, *Berg & Akkermans 1050* (F, K, MO, U); Aguarico, Parque Nacional Yasuni, Garza Cocha, *Ceron 4982* (MO). PERU. Soledad, *Tessmann 5175* (NY). UCAYALI: Coronel Portillo, Yarinacocha, Nueva Esperanza de Panaillo, *Vásquez 10500* (MO). LORETO: Manfinfa on upper Río Nanay, *Llewelyn Williams 1090* (F); Caballo-Cocha, *Llewelyn Williams 2273* (F, G); Maynas, Caballo-Cocha, *Ayala 3386* (MO, NY); Maynas, *Croat 17593* (F, MO, NY); Maynas, Puerto Almendras, *Díaz 241* (MO); Maynas, E of Pto. Alegria, *Gentry & Daly 18317* (MO, NY); Maynas, Río Mazan, ca. 35 km above Mazan, *Gentry & Revilla 16627* (F, MO, NY); Maynas, Tamshiyacu, *Gentry et al. 25807* (F, MO, NY); Maynas, Mishana, *Gentry et al. 25914* (MO, NY); Maynas, Río Nanay, *Gentry et al. 28959* (MO); Maynas, Quebrada Yahuasyacu, Caserio Portugal, *Grandez 1732* (MO); Maynas, Mishuyacu, *Klug 1301* (F, NY, US), *Klug 1372* (NY, US); Maynas, Mishana, *López 8634* (NY); Maynas, Río Nanay below Bellavista, *McDaniel 15243* (F, NY); Maynas, Río Momon above Bellavista, *McDaniel 20716* (MO, NY), *McDaniel 20753* (MO); Maynas, Río Atacuari, *Mori et al. 9227* (F, MO, NY); Maynas, Río Yaguasyaco, affluent of Río Ampiyaco, *Plowman 6908* (F); Maynas, Leticia, Isla Rondina, *Plowman et al. 6410* (F, GH); Maynas, Río Nanay, cerca a Santa Clara, *Revilla & Froehner 2532* (F, MO); Maynas, Río Yahuasyacu, *Revilla 742* (F, G, MO); Maynas, Alberque Selva Tours Río Momon, *Ruiz 1438* (MO); Maynas, Yanamono Explorama Tourist Camp, *van der Werff 9956* (MO); Maynas, Yanamono-Explorama Lodge, *Vásquez & Jaramillo 9138* (MO); Maynas, Iquitos, Caseria Nueva Jerusalem, Isla Iquitos, *Vásquez 11507* (MO); Requena, Jenaro Herrera, *Freitas 55* (MO); Requena, Río Tapiche, *Gentry et al. 21284* (MO); Requena, Jenaro Herrera, *Lamotte 0200* (MO), *Lamotte 085* (MO); Requena, Jenaro Herrera, Quebrada Iricahua, *Peters & Hammond 52/84* (F, MO, NY); Requena, Jenaro Herrera, *van der Werff 10050* (MO), *van der Werff 10066* (MO); Requena, Cocha Paucate, Río Ucayali near Pto. Peru, *Vásquez & Jaramillo 896* (F, G, MO, NY); Requena, Yarina (Río Tapiche), *Vásquez et al. 4858* (MO, NY); Ucayali, Yarinacocha (near Pucallpa), *Vásquez & Jaramillo 1520* (MO); Ucayali, Jenaro Herrera, Quebrada Supay, *Vásquez 12284* (MO).

*Pleurothyrium parviflorum* is one of the most frequently collected *Pleurothyrium* species. It is apparently a common tree in seasonally flooded forest (tahuampa) in Amazonian Peru and has been reported also from Brazil (Estado Acre and Amazonas) and Ecuador. This species can be easily identified by its habitat preference, and the combination of hollow stems (sometimes inhabited by ants), nearly glabrous inflorescence, glabrous leaves, and the reflexed margin of the tepals. There are a few other *Pleurothyrium* species with hollow twigs and tepals with reflexed margin and of those, *Pleurothyrium poeppigii* Nees can be confused with *P. parviflorum*. However, *P. poeppigii* has a dense, minute cover of hairs on the lower leaf surface, stiffer leaves, pubescent flowers and inflorescences, and smaller glands that do not enclose the outer stamens. One collection, *Nuñez 5901* (MO), is intermediate between the two. It resembles *P. parviflorum* in the lack of pubescence and the texture of the leaves and size of the glands, but has the stiffer, narrower infloresences and pubescence of the flowers found in *P. poeppigii*. Common name: Yacu Moena (= Moena del agua).

**Pleurothyrium pauciflorum** van der Werff & Hammel, sp. nov. TYPE: Costa Rica. Puntarenas: Cantón de Osa, ca. 2 km NE of the union of Río Pavón and Río Rincón, tree, 30 m, fl., *Hammel et al. 17909* (holotype, MO; isotypes, BM, CR, MEXU, USJ). Figures 34, 36.

Arbor, ad 35 m. Ramuli teretes, solidi, ferrugineo-tomentelli. Gemma apicalis ferrugineo-tomentella. Folia alterna, firme chartacea, 16–35 × 7–12 cm, oblonga vel elliptica, basi acuta vel obtusa, apice acumine ad 2 cm longo praedita, nervis lateralibus 14–20 utroque costae latere, brochidodroma in dimidio distale, supra glabra vel basi sparse tomentella, subtus pilis plus minusve erectis praedita, indumento secus nervos densiore, secus nervos majores tomentello; supra nervis immersis, subtus costa nervisque lateralibus prominenter elevatis, reticulatione paullo elevata. Petioli 1.8–3.2 cm longi. Inflorescentiae in bracteorum axillis ortae, ad 3 cm longae, pauciflorae. Pedicelli ad 2 mm longi. Flores ad 8 mm diametro, tepalis semi-erectis. Tepala 6, aequalia, crassa, 4–5 mm longa, ca. 4 mm lata, intus paullo papillosa, tres exteriora extus tomentella, tres interiora basi tomentella, demum papillosa. Stamina 9, 4-locellata, locellis lateralibus, glandulis perauctis, staminibus cingentibus. Pistillum ca. 3 mm longum, ovario pubescente sensim in stylum glabrum attenuato; receptaculo pubescente. Infructescentiae 2.5–4.5 cm longae; cupulae crassae, verrucosae, 2 cm longae, 3 cm latae, 1.5 cm profundae, tepalis frequenter persistentibus. Fructus ellipsoideus, 3 × 1.5 cm.

Tree, to 35 m tall. Twigs terete, solid, ferruginous-tomentellous, 4–6 mm diam. ca 5 cm below apex. Terminal buds ferruginous-tomentellous. Leaves alternate, grouped near tips of branches, firmly chartaceous, 16–35 × 7–12 cm, oblong or elliptic, the base acute or obtuse, tip acuminate, acumen to 2 cm long, but frequently damaged,

FIGURE 36. *P. pauciflorum.*—A. Habit.—B. Inflorescence with flower.—C. Fruit.

lateral veins 14–20 on each side, curving strongly upward near the margin and becoming loop-connected in upper half of the leaf, upper leaf surface glabrous or with traces of a tomentellous indument along midrib, the lower surface with ± erect hairs, this indument denser along veins and becoming tomentellous along major veins; veins immersed on upper surface, midrib and lateral veins prominently raised on lower surface, the tertiary venation slightly raised, but readily visible because of its indument. Petioles 1.8–3.2 cm long, upper surface flat, with similar indument as on twigs. Inflorescences in axils of (tardily) deciduous bracts, to 3 cm long, with up to 7 flowers (usually 3 or 1), ferruginous-tomentellous, bracts at base of inflorescences frequently present at anthesis, ovate or elliptic, to 5 mm long, pubescent on both surfaces. Pedicels ca. 2 mm long, ferruginous-tomentellous. Flowers ca. 8 mm diam., the tepals half-erect or somewhat spreading, never fully rotate; in old flowers tepals erect. Tepals 6, equal in size and shape, thick, 4–5 mm long, ca. 4 mm wide, all tepals inside slightly papillose, the outer 3 outside ferruginous-tomentellous, inner 3 with a basal triangular tomentellous area, otherwise slightly papillose. Stamens 9, all 4-celled, the cells lateral, glands strongly enlarged, enclosing stamens and fused. Pistil ca. 3 mm long, the pubescent ovary gradually narrowed into the glabrous style; receptacle ± pubescent. Infructescences 2.5–4.5 cm long, usually with 1 fruit; cupule thick, warty, ca. 2 cm tall, 3 cm wide and 1.5 cm deep, the tepals often persisting on the margin; fruit ellipsoid, ca. 3 × 1.5 cm. Fruits: June. Flowers: October. Elevation range: 50–200 m.

*Collections studied.* COSTA RICA. PUNTARENAS: Osa, *Hammel 17009* (MO); Osa, Reserva Indigena Guaimi, *Hammel 17909* (BM, CR, MEXU, MO, US).

*Pleurothyrium pauciflorum* can be readily identified by the ferruginous-tomentellous branchlets and the short, few-flowered inflorescences. Depauperate specimens of *P. golfodulcense* may also have short inflorescences, but this species has twigs covered with more or less appressed, ascending hairs, lacks erect hairs on the lower leaf surface, and has rotate flowers. It is uncommon to find a *Pleurothyrium* species with strongly enlarged glands that has half-erect tepals instead of rotate flowers. The androecium was, in all flowers seen, more or less covered by the tepals. Also, the tepals were, in comparison to other *Pleurothyrium* species, quite thick and fleshy. It would be interesting to discover what insect might pollinate this species; the arrangement of tepals suggests a beetle.

**Pleurothyrium pilosum** van der Werff, sp. nov.
TYPE: Panama. San Blas: Cangandi, 9°24′N, 70°24′W, hills near village, *de Nevers, Herrera & Charnely 7520* (holotype, MO; isotypes, CAS, PMA). Figure 34.

Arbor. Ramuli angulares, lateritio-tomentosi, cicatricibus conspicuis praediti. Gemma terminalis brevis, crassa, lateritio-tomentosa. Folia ad apices ramulorum congesta, chartacea, 15–25 × 7–13 cm, obovata, basi obtusa vel rotundata, apice rotundata vel breviter acuminata, nervis lateralibus 6  9 utroque costae latere, basalibus sub angulo acutiore quam venis distalibus abeuntibus, supra costa nervisque immersis, subtus elevatis, reticulatione paullo elevata; supra glabra, subtus dense pilosa, indumento secus costam nervosque tomentoso. Petioli 1.5–3 cm longi, lateritio-tomentosi. Inflorescentiae axillis cataphyllorum ortae, ad 15 cm longae, lateritio-tomentosae. Flores non visi. Tepala 6, late elliptica, 3 mm longa, intus et extus pubescentia. Stamina pubescentia, 9, 4-locellata, locellis lateralibus, glandulis magnis, stamina fere cingentibus, liberis. Pistillum glabrum, receptaculum pubescens. Fructus immaturus in cupula profunda, hexangulare inclusus.

Tree. Twigs angular, reddish brown tomentose, with conspicuous scars of old leaves, solid, 6 mm diam. ca. 5 cm below the tip. Terminal bud short, thick, reddish brown tomentose. Leaves clustered near tips of branches, chartaceous, 15–25 × 7–13 cm, obovate, the base obtuse to rounded, tip rounded or very shortly acuminate, lateral veins 6–9 on each side, the lowest pair leaving the midrib at the very base of the lamina and under a smaller angle than the more distal lateral veins, lateral veins approaching the leaf margin very closely and strongly arching upward, but only the upper 2 or 3 veins loop-connected, midrib and lateral veins immersed on upper leaf surface, but prominently raised on lower surface, the tertiary venation slightly raised; upper surface glabrous or with very few scattered reddish hairs, lower surface densely covered with erect, reddish hairs, these not obscuring the surface, the indument becoming tomentose along lateral veins and midrib. Petioles flattened above, 1.5–3 cm long, reddish brown tomentose. Pubescence on twigs and veins on lower leaf surface described by collectors as orange. Inflorescences in axils of cataphylls, at tips of branches, to 15 cm long, reddish brown tomentose, branchlets once cymosely branched or flowers racemosely arranged. Open flowers not seen. Tepals (based on remnants on young fruits) broadly elliptic, densely pubescent on both surfaces, 3 mm long. Stamens pubescent, 9, 4-celled, cells lateral; glands en-

larged, forming a dome and largely enclosing stamens, free (the glandular mass is broken up in fruiting stage). Ovary and style glabrous; receptacle pubescent inside. Young fruits enclosed in cupule, cupule with 6 ribs, to 1.5 cm long. Young fruits: March. Elevation range: ca. 30 m.

*Collection studied.* PANAMA. SAN BLAS: Cangandi, *de Nevers et al. 7520* (CAS, MO, PMA).

*Pleurothyrium pilosum*, only known from the type collection from San Blas, Panama, is closely related to *P. racemosum*, another Panamanian species only known from the type. These two species have in common a glabrous ovary and style, pubescent receptacle, clustered leaves, the basal lateral vein leaving the midrib under an acute angle at the very base of the lamina, and lateral veins that approach the leaf margin very closely. Although some of these characters occur also in other *Pleurothyrium* species, the ascending basal lateral veins are unique to these two species. *Pleurothyrium pilosum* differs from *P. racemosum* in its larger leaves (to 25 vs. 14 cm), in its leaf shape (obovate vs. oblong), indument of lower leaf surface (pilose vs. with scattered curled hairs or subglabrous) and indument of twigs (longer, red-brown vs. shorter plain brown).

Unfortunately, the only collection of *Pleurothyrium pilosum* is in young fruit. The description of floral parts is based on dried remnants on the young fruits, and I am not certain that the dimensions are correct. Because the type collection was made from a marked tree in a permanent quadrat, it is likely that the tree will be recollected in the future.

**Pleurothyrium poeppigii** Nees, Syst. laur.: 349. 1836. *Octoea poeppigii* (Nees) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Peru. Maynas: *Poeppig addenda 301* (B, G, GZU, L, holotype not designated). Figure 37.

*Pleurothyrium krukovii* A. C. Smith, Phytologia 1: 121. 1935. *Ocotea krukovii* (A. C. Smith) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Brazil. Acre: near mouth of Rio Macauhan, *Krukoff 5563* (holotype, NY not seen; isotypes A, G, K, MO).

Tree to 30 m tall. Twigs terete or subangular, fistulose, minutely brown-tomentellous or glabrous, 4–7 mm diam. ca. 5 cm below the tip. Terminal bud minutely brown-tomentellous. Leaves alternate, firmly chartaceous or subcoriaceous, 20–30 × 6–10 cm, (narrowly) elliptic to slightly (narrowly) obovate, the base acute, tip rounded or shortly acute, the upper surface glabrous, lower surface minutely tomentellous, papillose or rarely glabrous, lateral veins 14–18 on each side, arching upward near the margin, not or very weakly loop-connected, venation immersed on the upper surface, midrib and lateral veins raised on the lower surface. Petioles 1.5–2 cm long, with similar indument as on twigs, canaliculate. Inflorescences in axils of deciduous bracts, or infrequently in axils of regular leaves, to 18 cm long, minutely tomentellous or subglabrous, the branchlets complanate, to two times cymosely branched, the flowers often appearing densely clustered; bracts deciduous at anthesis. Pedicels 2–3 mm long. Tepals 6, equal, ± erect at anthesis, the margin reflexed, elliptic, ca. 2 mm long, the outer three minutely tomentellous outside, the inner three with a minutely tomentellous, triangular, basal patch, otherwise papillose; all tepals papillose on inner surface. Flower color described as white, green, and dull orangish; odor of melon. Stamens 9, all 4-celled, glabrous, 2 cells ± extrorse, the other 2 ± introrse, filaments about as long as anther, outer stamens separated by the enlarged glands, but glands not surrounding stamens and remaining free. Ovary ellipsoid, mostly included in the glabrous receptacle, glabrous or papillose near the tip, the style about as long as ovary, papillose; pistil ca. 2 mm long. Cupule cup-shaped, ± warty, ca. 1.5 cm high, 1.8 cm wide. Fruits: January, August, and November. Flowers: March, April, August, and December. Elevation range: 400–1,800 m.

*Collections studied.* BOLIVIA. COCHABAMBA: Totora, Yungas of Janamayu, *Cardenas 3966* (F, US). BRAZIL. ACRE: mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff 5255* (A, F, G, MO, NY, S, US); near mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff 5263* (S); mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff 5563* (A, G, K, MO), *Krukoff 5722* (A, NY). COLOMBIA. PUTUMAYO: along Rumiyaco River, above confluence with Rio Mocoa, *Soejarto 1268* (GH). ECUADOR. NAPO: road to Puerto Napo–Tena, *Lugo 320* (S); 7–16 km E of Puerto Napo, *Neill 6555* (F, MO, NY); along road to Tena, 2 km from Misahualli, *Palacios 2775* (MO); Jatun Sacha, 8 km abajo de Puerto Misahualli, *Palacios 982* (MO); Tena, *Neill 7603* (MO). PERU. *Ruíz & Pavón s.n.* (F). LORETO: Maynas, Yurimaguas, *Poeppig Addenda 301* (B, G, GZU, LE). MADRE DE DIOS: Cocha Cashu Biological Station, Manu National Park, *Gentry 43560* (MO, NY); Manu, Río Manu, Cocha Cashu Station, *Davidson 85-19* (F); Manu, Cerro de Pantiacolla, Río Palatoa, *Foster 10642* (MO); Manu, Río Manu, *Foster 3153* (F, MO); Manu, Cocha Cashu uplands, Manu Park, *Nuñez 5901* (MO). PASCO: around Oxapampa, *van der Werff 8343* (MO), *van der Werff 8345* (MO); Oaxapampa, 5 km SE of Oxapampa, *Smith 2793* (MO); Oxapampa, around Villa Rica, *van der Werff 8288* (MO).

FIGURE 37. Distribution of *P. poeppigii* (★), *P. racemosum* (●), *P. steyermarkianum* (○), and *P. synandrum* (■).

As accepted here, *P. poeppigii* is a wide-ranging species occurring in Amazonian Brazil, Bolivia, Peru, Ecuador, and Colombia. Its nearest relative is *P. parviflorum* Ducke, from which it differs in the tomentellous flowers and inflorescences, the narrower inflorescences, the tomentellous lower leaf surfaces, and the more coriaceous and generally larger leaves. The type specimens of *P. poeppigii* and *P. krukovii* are both somewhat atypical for this species. *Poeppig addenda 301*, the type of *P. poeppigii*, has strongly fistulose twigs and even some of the inflorescences are fistulose. These inflorescences are shorter and more compact than nonfistulose inflorescences on other specimens. The flowers of *Poeppig addenda 301* are slightly larger than on the other specimens, and the pedicels are slightly thicker. However, I feel that these differences do not warrant the recognition of two species, and I am inclined to accept most of these differences as a consequence of the strongly fistulose character of twigs and inflorescences. Oddly enough, none of the labels indicate that the twigs were inhabited by ants, although the hollow twigs and the exit holes along the twigs strongly suggest that ants colonize the twigs. See also discussion under *P. cuneifolium*.

The type of *P. krukovii* has, for this species, rather thin and glabrous leaves, characters found in *P. parviflorum*. The inflorescence and the flower buds have, however, the indumentum of *P. poeppigii*. In spite of the fact that A. C. Smith described flowers of *P. krukovii*, none of the isotypes I have seen had flowers, and the microfiche photo of the NY holotype does not show flowers either. *Krukoff 5722*, a paratype, also has glabrous leaves, but has tomentellous flowers. *Krukoff 5255* has stiffer leaves and tomentellous leaves and flowers; it fits my concept of *P. poeppigii* very well. These observations allow two approaches. One is to define three species narrowly: *P. poeppigii*, only known from its type; *P. krukovii*, with very few collections (excluding, for instance, *Krukoff 5255*) and defined by its glabrous, chartaceous leaves and subglabrous inflorescence axes; and a third, undescribed species occurring in Brazil, Peru, Ecuador, and Colombia with subcoriaceous, tomentellous leaves and rather

lax inflorescences. The other approach is to accept *P. poeppigii* in a wider sense, defined by its fistulose stems, tomentellous flowers, narrow inflorescences, and similar floral structure. I take this approach rather than recognizing three poorly defined and hard to identify taxa.

For the same reason, the collection *Cardenas 3966* (F, US) is included in *Pleurothyrium poeppigii*, although its obovate leaves are aberrant for this species. In other characters, such as flower size and structure, fistulose and tomentellous twigs, it fits in *P. poeppigii*, and I am not willing to describe a new taxon with only one collection based solely on a different leaf shape. This is the only collection of *P. poeppigii* from Bolivia.

In addition to *Pleurothyrium parviflorum* Ducke and *P. poeppigii*, *P. cuneifolium* Nees can also have fistulose twigs. This latter species can be recognized by its angular, lenticellate twigs, larger flowers, and tepals that are glabrous on the inner surface.

Although most collections of *Pleurothyrium poeppigii* are from lowland sites, I include here three collections from the Oxapampa area in central Peru from ca. 1,800 m elevation.

**Pleurothyrium prancei** van der Werff, sp. nov. TYPE: Brazil. Acre: vicinity of Serra de Moa, varzea forest, stilt-rooted tree, 8 m tall, *Prance et al. 12392* (holotype, F; isotypes, F, MO, NY, S). Figure 32.

Arbor, ad 8 m. Ramuli parum angulati, cinnamomeo-tomentelli; glabrescentes. Gemma terminalis cinnamomeo-tomentosa. Folia alterna, chartacea, 15–30 × 4.5–9 cm, anguste obovata vel anguste elliptica, basi acuta, apice acuminata, acumine ad 1.5 cm longo, supra glabra, subtus costa et nervis tomentellis, laminis glabris vel paucis pilis praeditis, supra venatione immersa, subtus costa nervisque elevatis, reticulatione paullo elevata; nervis 9 12 utroque costae latere, sursum arcuatis, venatione brochidodroma in dimidio distale. Petioli 2–3 cm longi. Inflorescentiae axillis cataphyllorum ortae, in apicibus ramulorum congestae, cinnamomeo-tomentellae, 10 20 cm longae, ramulis semel, raro bis cymae more furcatis, bracteis sub anthesi deciduis. Pedicelli 5–10 mm longi. Flores intus virides, 8–9 mm diametro. Tepala 6, subaequalia, patentia, margine plano, tres exteriora late elliptica 4 × 3 mm, extus cinnamomeo-tomentella, intus maxime basi pubescentia et zona peranguste centrali papillosa, demum glabra; tres interiora elliptica, 3 × 2 mm, extus parte triangulari basali tomentella, demum glabra, intus dense papillosa. Stamina 9, 4-locellata, locellis lateralibus, filamentis stamina aequantibus, glabris; glandulis incrassatis, vix stamina cingentibus, liberis. Pistillum ca. 2 mm longum, pubescens, ovario sensim in stylum brevem attenuato, stigmate incrassato. Fructus ignotus.

Tree, to 8 m tall, with stilt roots fide collectors. Twigs slightly angular, brown-tomentellous, glabrescent, 4 mm diam. ca. 5 mm below tip. Terminal bud brown-tomentellous. Leaves alternate, chartaceous, 15–30 × 4.5–9 cm, narrowly obovate to narrowly elliptic, the base acute, the apex acuminate, acumen to 1.5 cm long, but usually broken off, glabrous above, midrib and to a lesser degree lateral veins tomentellous below, the lamina glabrous or with a few scattered hairs near the base, venation immersed on upper surface, midrib and lateral veins raised on lower surface, tertiary venation slightly raised; lateral veins 9–12 on each side, arching upward near the margin and loop-connected in the distal half. Petioles 2–3 cm long, ± terete, with a similar indument as on twigs. Inflorescences in axils of cataphylls near tip of twigs, brown-tomentellous, 10–20 cm long, the branchlets once or rarely twice cymosely branched, bracts deciduous at anthesis, those subtending buds ca. 2 mm long, tomentellous outside, glabrous inside. Pedicels 5–10 mm long, brown-tomentellous. Flowers green inside, 8–9 mm diam. Tepals 6, subequal, spreading, the margin plane, the outer 3 broadly elliptic, 4 × 3 mm, brown-tomentellous outside, glabrous inside, except for some hairs near the very base and a narrow, median, papillose strip; inner 3 elliptic, 3 × 2 mm, the outside with a basal, triangular, tomentellous patch, otherwise glabrous, the inside densely papillose. Stamens 9, 4-celled, the cells lateral, opening back-to-back, filaments about as long as anther, glabrous; glands enlarged, protruding between the outer stamens and touching adjoining gland in front of outer stamens, but free. Pistil ca. 2 mm long, the ovary pubescent, gradually narrowed into the short style, stigma enlarged. Floral tube pubescent inside. Fruits unknown. Flowers: April. Elevation range: ca. 100 m.

*Collection studied.* BRAZIL. ACRE: Cruzeiro do Sul, vicinity of Serra da Moa, *Prance 12392* (F, MO, NY, S).

*Pleurothyrium prancei*, only known from the type collection, occurs in varzea (flooded forest) and reportedly has stilt roots, very unusual for a Lauraceae. It is characterized by the combination of glabrous, alternate leaves, a pubescent pistil, and flowers with the outer tepals glabrous inside, and inner tepals papillose inside. *Pleurothyrium prancei* does not seem to have close relatives. *Campbell et al. 8057*, from the upper Rio Moa in Acre, Brazil is possibly this species; the specimen is, however, sterile and hence the identification tentative.

It is a pleasure to name this species after Ghillean Prance, who has contributed so widely to the knowledge of the Amazonian flora.

**Pleurothyrium racemosum** van der Werff, sp. nov. TYPE: Panama. Panama: Cerro Jefe, along summit road and trail into Chagres Valley, elev. 900 m, *McPherson 12120* (holotype, MO; isotypes, BM, F, HBG, MEXU, PMA). Figures 37, 38.

Arbor parva, ad 7 m alta. Ramuli teretes, hornotini castaneo-tomentosi, annotini cinereo-tomentosi. Folia ad apices ramulorum aggregata, firme chartacea, 6 14 × 2.5–4 cm, oblonga vel leviter obovata, basi truncata vel acuta, apice obtusa vel breviter acuta, supra glabra vel basi costae nervorumque paullo castaneo-tomentosa, subtus pilis castaneis praedita basi costae nervorumque et margine tomentosa. Nervi laterales utroque costae latere 6–9, venatione brochidodroma in dimidio distale. Inflorescentiae ex axillis bractearum ortae, castaneo-tomentosae, 3–7 cm longae, ob abortionem florum lateralium racemosae. Tepala 6, aequalia, elliptica, ca. 4.5 mm longa, rotata vel paullo reflexa. Stamina 9, 4-locellata, antheris introrsum flexis, locellis lateralibus, filamentis pubescentibus. Glandulae stamina exteriora cingentes, liberae. Ovarium anguste ellipsoideum, glabrum; stylus glaber, stigmate peltato. Tubus floralis profundus, pubescens. Fructus ignoti.

Small tree, to 7 m tall. Twigs terete, solid, brown-tomentose when young, the tomentum turning gray on older twigs, the demarcation between brown and gray tomentum sharp, diameter of the young twigs ca. 3 mm. Terminal bud brown-tomentose. Leaves clustered near tips of branches, firmly chartaceous, 6–14 × 2.5–4 cm, oblong or somewhat obovate, the base truncate or acute, the tip obtuse or slightly acute, the upper surface glabrous or with some scattered brown hairs, these concentrated along the base of the midrib and lateral veins, the lower surface with more brown hairs becoming tomentose along the base of the midrib, lateral veins and margin. Venation, including midrib, immersed on upper surface, raised on lower surface; lateral veins 6–9 on each side, curving toward the tip near the margin and venation becoming brochidodromous in the distal half of the laminae. Basal veins leaving midrib under a more acute angle than more distal veins, and situated at the very base of the lamina. Petioles brown tomentose, 9–12 mm long. Inflorescences in the axils of cataphylls at the tip of the branches, brown tomentose, 3–7 cm long, racemose, 4–10 flowers per inflorescence; individual flowers representing a dichasium with the lateral flowers undeveloped, this indicated by 2 bracts at the transition from peduncle to pedicel. Peduncle to 10 mm long, pedicel to 3 mm long, both brown tomentose. Flowers brown outside, creamy-white inside, 9 mm diam. Tepals 6, equal in size, 4.5 mm long, elliptic, spreading to reflexed at anthesis; outer tepals brown-tomentose outside, with a triangular, gray-tomentose patch inside, otherwise papillose; inner tepals with a triangular, brown-tomentellous patch, otherwise glabrous outside, gray-tomentellous inside. Stamens 9, all 4-celled, the anthers curved inward, the cells lateral; filaments pubescent. Bases of filaments united, forming a ridge carrying the free parts of the stamens and the glands. Staminal glands enclosing the outer stamens, but not fused. Ovary narrowly ellipsoid, glabrous, 1 mm long; style glabrous, 1 mm long; stigma peltate. Floral tube deep, densely pubescent inside. Fruits and cupule unknown. Flowers: February.

*Collection studied.* PANAMA. PANAMA: Cerro Jefe, *McPherson 12120* (BM, F, HBG, MEXU, MO, PMA).

The type (and only) collection of *Pleurothyrium racemosum* was made on Cerro Jefe in Panama, a low mountain about 800 m high, which has yielded many endemics. The indument on the lower leaf surface can be rather sparse, especially on older leaves, but remnants of the characteristic curled hairs are always present near the base of the leaf and along the major veins. This species is closely related to *P. pilosum*, where differences between these species are discussed.

**Pleurothyrium steyermarkianum** Allen, Mem. New York Bot. Gard. 15: 93. 1966. TYPE: Venezuela. Mérida: La Azulita, forest above Hacienda Agua Blanca, elev. 1,310–1,340 m (fl), *Steyermark 56077* (holotye, F not seen; isotype, VEN). Figures 37, 39.

Tree, to about 20 m tall. Twigs angular, solid, minutely tomentellous when young, becoming glabrous with age, 4–5 mm diam. about 4 cm below apex. Leaves alternate, coriaceous, 12–25 × 5–10 cm, elliptic to broadly elliptic, base acute or obtuse, apex acute or acuminate, glabrous and somewhat shiny above, with scattered, appressed hairs or glabrous below, lateral veins 11–16 on each side, curving upward near the margin and weakly loop-connected in the distal half of lamina, midrib and lateral veins immersed on upper surface, raised on lower surface, tertiary venation scarcely visible on upper surface, slightly raised on lower surface. Petioles canaliculate, 1.1–2.5 cm long. Inflorescences in axils of deciduous bracts, to 16 cm long, minutely and laxly brown-tomentellous, the branchlets 2–3 times cymosely branched, bracts subtending the flower buds broadly ovate, boat-shaped, tomentellous outside and glabrous inside. Pedicels to 2 mm long, tomentellous, thick, acutely triangular in cross section, the three ribs continuing as keels on the outer 3 tepals.

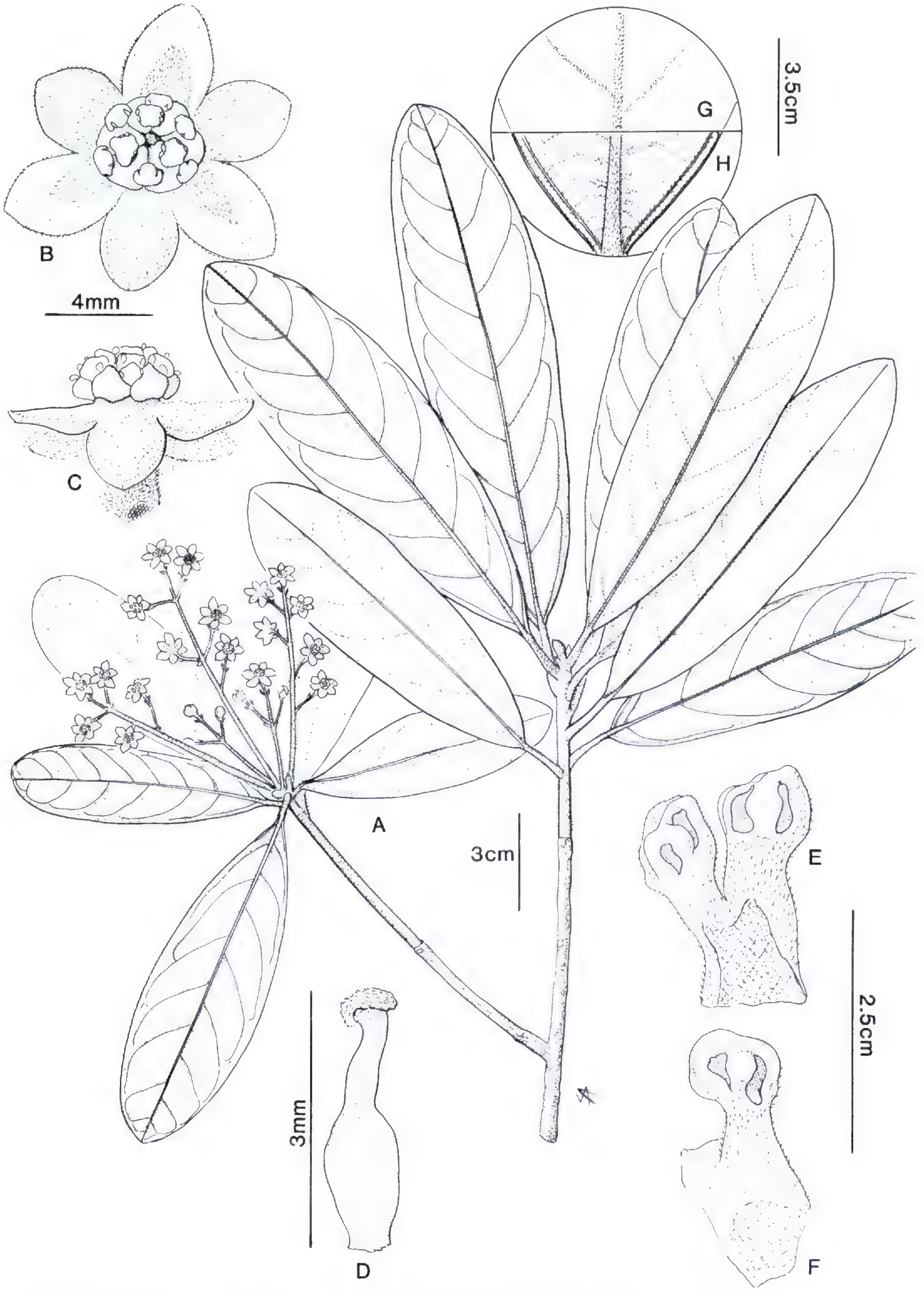



FIGURE 38. *P. racemosum*. —A. Habit. —B. Flower. —C. Flower, side view. —D. Pistil. —E. Stamens I and III. —F. Stamen II. —G. Detail of upper leaf surface. —H. Detail of lower leaf surface.

FIGURE 39. *P. steyermarkianum.*—A. Habit.—B. Flower.—C, D. Stamens.—E. Pistil.—F. Petiole.—G. Reticulation pattern on leaf.—H. Part of inflorescence.—I. Underside of leaf base.—J. Detail of lower leaf surface.

Flowers ca. 8 mm diam., pale yellow-green and fragrant fide collectors. Tepals 6, elliptic, 3–3.5 mm long, papillose inside, the outer 3 tomentellous outside, the inner 3 with a central tomentellous strip, otherwise glabrous outside. Stamens 9, 4-celled, the cells lateral; glands enlarged, forming ridges surrounding the stamens, fused. Pistil and receptacle glabrous, ovary ellipsoid. Cupule cup-shaped, 2 cm wide, 1 cm high; fruit ellipsoid, ca. 2 × 1.5 cm. Flowers: April. Elevation range: 1,300–2,000 m.

*Collections studied.* VENEZUELA. MERIDA: Selva nublada de la Zona La Trampa, *Bernardi 2169* (G, MER, NY); La Azulita, *Steyermark 56077* (VEN).

*Pleurothyrium steyermarkianum* is only known from two collections made in the Andes of Venezuela. The floral structure, especially the way in which the enlarged glands form ridges surrounding the stamens, the triangular or three-ribbed pedicels, and broad bracts of the inflorescence suggest a relationship with *P. cuneifolium* and its allies. However, *P. steyermarkianum* has a characteristic leaf

indument, lacks fistulose twigs, and differs in floral dimensions from *P. cuneifolium*.

When publishing *Pleurothyrium steyermarkianum* (as *P. steyermarkiana*), Allen indicated that the holotype was deposited in NY. This is an error. The holotype was at F and no isotype was found at NY. The F holotype was sent on loan from F to MO, but unfortunately never arrived and presumably is lost. The only specimen of the type collection studied is the VEN isotype.

Allen also indicated the collection *Bernardi 2169* had flowers and fruits. All sheets I have seen, however, have floral buds and fruits; thus, the only specimen of *P. steyermarkianum* with flowers is the VEN isotype.

**Pleurothyrium synandrum** van der Werff, sp. nov. TYPE: Colombia. Valle: Río Calima, La Trojita, *Cuatrecasas 16656* (holotype, F; isotypes, U, US). Figures 37, 40.

Arbor, ad 30 m. Ramuli teretes, ferrugineo-tomentulosi, glabrescentes. Gemma terminalis dense ferrugineo-pubescens. Folia alterna, coriacea, elliptico-ovata vel elliptica, 15–25 × 6–8 cm, basi et apice acuta, supra glabra, subtus ferrugineo-tomentosa vel tomentella, paucis pilis longioribus secus costam et venas laterales praedita; supra venatione immersa, subtus costa venisque lateralibus elevatis; venis lateralibus 18–24 utroque costae latere, marginem versus arcuatis, sed non connexis. Petioli ca. 1 cm longi, ferrugineo-tomentulosi. Inflorescentiae ex axillis bractearum ortae, 8–15 cm longae, ferrugineo-tomentulosae, paniculatae, ramulis 2–3 plo cymae more divisis. Flores pallide flavi, 11–12 mm diametro. Tepala 6, aequalia, 5 mm longa, intus papillosa, exteriora extus pubescentia, interiora minute puberula praeter basim pubescentem. Stamina 9, 4-locellata, 6 exteriora duobus locellis extrorsis, duobus lateralibus, 3 interiora locellis extrorsis, filamentis staminum exteriorum dorsaliter pubescentibus; interiora arcte stylum pubescentem cingentia. Glandulae dilatatae sed stamina exteriora vix ambientes. Cupula 4–5 cm late, 2.5 cm alta, verrucosa; fructus ovoideus, 4 × 2.5 cm.

Tree, 30 m tall. Twigs terete, solid, the tip with brown slender spreading hairs, brown-tomentulose on older parts, the indument wearing off on older parts, diameter of twig 6–8 mm 5 cm below tip. Terminal bud densely brown pubescent. Leaves alternate, coriaceous, elliptic-ovate to elliptic, 15–25 × 6–8 cm, base and apex acute, the upper surface glabrous, lower surface ferruginous-tomentose or tomentulose with some longer hairs along midrib and lateral veins; venation immersed on upper surface, midrib and lateral veins raised on lower surface; lateral veins 18–24, closely spaced, arching toward apex near the margin, but not connected with their superior vein. Petioles ca. 1 cm long, brown-tomentulose, broadly canaliculate, ca. 4 mm diam. Inflorescences in the axils of cataphylls, 5–15 cm long, paniculate, the branchlets 2–3 times cymosely branched, brown-tomentellous, 40–60 flowers per inflorescence, bracts mostly deciduous at anthesis, ca. 3 mm long, elliptic, brown-pubescent outside, glabrous inside. Flowers pale yellow, 11–12 mm diam. Tepals 6, equal, elliptic, 5 mm long, papillose on inside, outer tepals pubescent outside, inner ones minutely puberulous except for the pubescent base. Stamens 9, 4-celled, the outer 6 with one pair of cells extrorse, the other pair introrse; inner stamens with extrorse cells; filaments of outer stamens dorsally pubescent; filaments and anthers of inner 3 stamens poorly differentiated, the stamens forming a tight cylinder around the brown-pubescent style. Glands enlarged, protruding between the outer stamens, but these scarcely enclosing, free. Receptacle pubescent inside. Cupule, when pressed, 4–5 cm diam., ca. 2.5 cm tall, warty fruit ovoid, 4 × 2.5 cm when dry. Flowers and fruits: March. Elevation range: ca. 50 m.

*Collection studied.* COLOMBIA. VALLE: Río Calima, La Trojita, *Cuatrecasas 16656* (F, U, US).

*Pleurothyrium synandrum* is only known from the type collection from near the coast in Depto. Valle, Colombia. This species can immediately be recognized by its ovate-elliptic leaves with the numerous lateral veins close together and its unusual floral structure. In other *Pleurothyrium* species with strongly enlarged glands, not only do the glands grow outward, but also sideways and somewhat inward and the inner three stamens are therefore separated from each other by glandular tissue. Frequently, the glandular mass covers the upper part of the ovary and surrounds the style, while the lower part of the ovary is sunk in the floral tube. In *P. synandrum* the inner three stamens completely surround the style and the glandular tissue does not take part in protecting the pistil. The androecium of this species contains much mucilage, which makes the dried flowers very hard and brittle, whereas after boiling the flowers the parts become soft and slimy; I could therefore not make sure whether the inner stamens were actually (partly) fused or merely tightly pressed together. Another unusual feature of *P. synandrum* is that the basal pair of locelli on the outer stamens has virtually become extrorse. The glandular mass in this species shrinks strongly upon drying, and the outer stamens are raised much higher above the glands in dried flowers than in boiled flowers.

**Pleurothyrium tomentellum** van der Werff, sp. nov. TYPE: Ecuador. Pastaza: Pozo petrolero "Golondrina" de Petro-Canada, 30 km NW of Curaray, elev. 400 m, tree, 15 m, 10

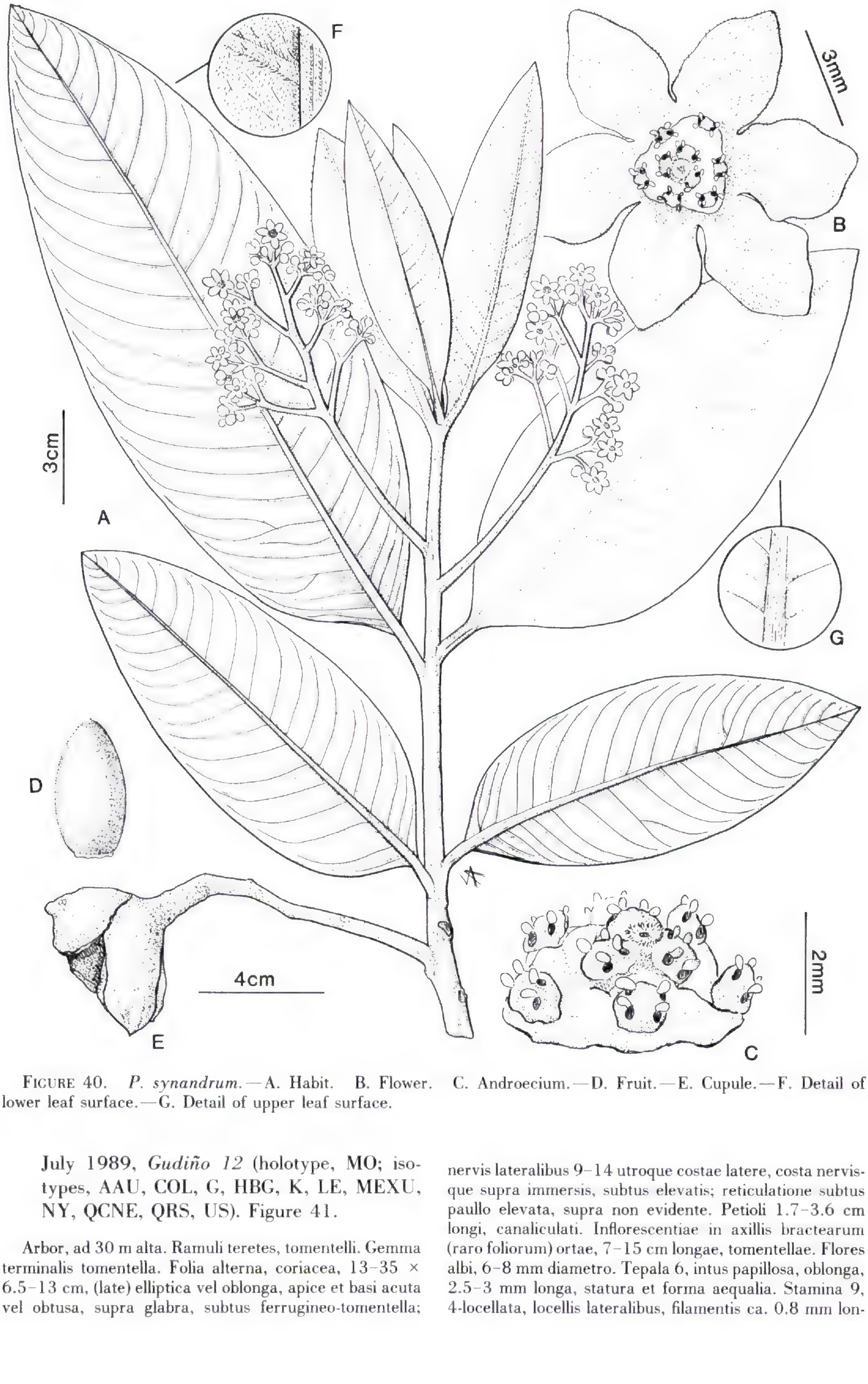



FIGURE 40. *P. synandrum.*—A. Habit. B. Flower. C. Androecium.—D. Fruit.—E. Cupule.—F. Detail of lower leaf surface.—G. Detail of upper leaf surface.

July 1989, *Gudiño 12* (holotype, MO; isotypes, AAU, COL, G, HBG, K, LE, MEXU, NY, QCNE, QRS, US). Figure 41.

Arbor, ad 30 m alta. Ramuli teretes, tomentelli. Gemma terminalis tomentella. Folia alterna, coriacea, 13–35 × 6.5–13 cm, (late) elliptica vel oblonga, apice et basi acuta vel obtusa, supra glabra, subtus ferrugineo-tomentella; nervis lateralibus 9–14 utroque costae latere, costa nervisque supra immersis, subtus elevatis; reticulatione subtus paullo elevata, supra non evidente. Petioli 1.7–3.6 cm longi, canaliculati. Inflorescentiae in axillis bractearum (raro foliorum) ortae, 7–15 cm longae, tomentellae. Flores albi, 6–8 mm diametro. Tepala 6, intus papillosa, oblonga, 2.5–3 mm longa, statura et forma aequalia. Stamina 9, 4-locellata, locellis lateralibus, filamentis ca. 0.8 mm lon-

FIGURE 41. Distribution of *P. tomentellum* (★), *P. tomiwahlii* (●), *P. undulatum* (○), and *P. westphalii* (■).

gis, glandulis incrassatis, stamina cingentibus, contiguis, non connatis. Ovarium glabrum, in stylo attenuatum; tubo florale intus tomentello. Fructus ellipsoideus, 3 × 1.5 cm, cupula verrucata, 2 cm lata, 1 cm profunda.

Tree, to 30 m tall. Twigs terete, smooth or finely ridged, brown-tomentellous, solid, 4–7 mm diam. ca. 5 cm below tip. Terminal bud brown-tomentellous. Leaves alternate, coriaceous, 13–35 × 6.5–13 cm, elliptic, broadly elliptic or oblong, the tip and base acute or obtuse, upper surface glabrous, opaque, lower surface densely rufous-tomentellous or coarsely papillose, the surface completely covered by the indument; lateral veins 9–14 on each side, arching upward near the margin, but not loop-connected; midrib and lateral veins immersed on upper surface, raised on lower surface; tertiary venation (very) weakly raised on lower surface, not visible on upper surface. Petioles 1.7–3.6 cm long, canaliculate to deeply canaliculate, with similar indument as twigs. Inflorescences in axils of deciduous bracts, rarely in axils of leaves, to 7–15 cm long, the branchlets to 4 times dichotomously branched, rufous-tomentellous, bracts mostly deciduous at anthesis, if present tomentellous outside and subglabrous or tomentellous inside. Pedicels 2–6 mm long, rufous-tomentellous. Flowers 6–8 mm diam. Tepals 6, white, papillose-puberulous on inside, oblong, 2.5–3 mm long, equal in size and shape. Stamens 9, 4-celled, the cells lateral, the filaments ventrally pubescent, filaments ca. 0.8 mm long. Glands strongly enlarged, completely surrounding the stamens, but not fused. Pistil glabrous, 1.5 mm long, ovary gradually narrowed into the style, style and ovary of the same length; floral tube densely tomentellous within. Fruit ellipsoid, 3 × 1.5 cm, cupule cup-shaped, warty, 2 cm wide, 1 cm tall. Flowers: January–July. Fruits: January.

Common name (Huaorani): Ontumo.

*Collections studied.* ECUADOR. MORONA-SANTIAGO: 35 km NE from Montalvo, *Zak 4459* (MO, QCNE). PASTAZA:

30 km NWE of Curaray, *Gudiño 12* (AAU, COL, G, HBG, LE, K, MEXU, MO, NY, QCNE, QRS, US); 30 km NE from Curaray, *Gudiño 17* (MO, QCNE); 115 km S of Coca, near Río Tiguino, *Hurtado 1464* (MO, QCNE); Via Auca, 115 km S of Coca, *Neill 8741* (MO, QCNE); 115 km S of Coca, near Río Tiguino, *Neill & Hurtado 8783* (MO, QCNE), *Rubio 56* (MO, QCNE); 110 km S of Coca, 10 km from Río Tiguino, *Palacios 3416* (MO, QCNE). PERU. HUANUCO: Pachitea, Pucallpa region, 24 km SE of Puerto Inca, *Wallnoefer 18-29788* (MO).

*Pleurothyrium tomentellum* is a species with a limited distribution, known only from the Amazonian lowlands of Ecuador, from areas that recently became accessible due to oil exploration, and one collection from Amazonian Peru. According to the label data of *Neill & Hurtado 8783*, the species is locally very common. *Pleurothyrium tomentellum* can be readily identified by the combination of its tomentellous leaves and small (6–8-mm-diam.) flowers. Noteworthy are also the glabrous pistil, pubescent receptacle, and rather small cupule. In leaf characters (texture, indument, lack of marginal vein) and its short inflorescence it resembles *P. palmanum* from Costa Rica, but that species has larger flowers, broader, more or less obovate leaves, and a glabrous receptacle. Most collections have tomentellous lower leaf surfaces and inflorescence bracts that are tomentellous on both surfaces. The type collection has a shorter indument on the leaves, approaching the papillose condition, and the inner surface of the inflorescence bracts is subglabrous. In floral characters the collections are identical (only the sole Peruvian collection has a sparser indument on inner surface of tepals), and the differences mentioned are too weak for recognition of two taxa. Moreover, the type was collected together with a specimen with the slightly longer indument (*Gudiño 12, 17*).

**Pleurothyrium tomiwahlii** van der Werff, sp. nov. TYPE: Ecuador. Los Ríos: Centinela Ridge, elev. 600 m, 16 July 1991, *van der Werff et al. 12365* (holotype, MO; isotypes, AAU, B, BR, C, COL, E, F, G, GH, HBG, K, KUN, LE, MEXU, MY, QCNE, QRS, S, SEL, U, US). Figures 41, 42.

Arbor, 20 m. Ramuli crassi, teretes, juvenales ferrugineo-tomentosi, vetustiores glabrescentes. Gemma terminalis tomentosa. Folia ad apices ramulorum aggregata, chartacea, laminis 11–40 × 6–17 cm, basi obtusis vel acutis, apice rotundatis, obtusis vel breviter acuminatis, (late) obovatis vel (late) ellipticis, utrinque glabris vel paucis pilis erectis praeditis; nervis lateralibus 8–10 utroque costae latere. Petioli 2.5–6 cm longi, base incrassati, canaliculati. Inflorescentiae ex axillis bractearum ortae, tomentosae, paniculatae ramulis semel (raro bis) cymose ramosis, 7–12 cm longae, bracteis sub anthesi deciduis. Tepala 6, aequalia, extus pubescentia, 3 interiora intus pubescentia, 3 exteriora intus praeter partem triangularem basalem glabra vel papillosa, sub anthesi reflexa, ca. 4 mm longa, elliptica. Stamina 9, 4-locellata, locellis lateralibus, filamentis pubescentibus, parte basale in tubo coalitis; glandulis magnis inter stamina exteriora protrudentibus. Ovarium gracile, glabrum, sensim in stylum attenuatum; receptaculo et tubo filamentorum intus pubescente. Frutus ignotus.

Tree, to 20 m tall. Twigs ± terete, solid, with pale bark, the young growth ferruginous-tomentose, soon glabrescent, ca. 8 mm diam. 5 cm below tip. Terminal bud brown tomentose. Leaves clustered near tips of branches, alternate, chartaceous, laminae 11–40 × 6–17 cm, the base obtuse or acute, the tip rounded, obtuse or shortly acuminate, (broadly) obovate, or (broadly) elliptic; glabrous on both surfaces or with scattered erect hairs, these mostly along the major veins or near base of the lamina; lateral veins 8–10 on each side; venation immersed on upper surface or weakly raised, midrib and lateral veins raised on lower surface. Petioles 2.5–6 cm long, strongly canaliculate, the base swollen, with similar indument as on the twig. Inflorescences in the axils of cataphylls near the tips of branches, tomentose, paniculate, the lateral branchlets once cymosely branched, 7–12 cm long, bracts deciduous at anthesis. Flowers cream-colored, fragrant. Tepals 6, equal in shape, densely pubescent outside, the inner three densely pubescent inside, outer three with a basal, triangular, pubescent patch, otherwise glabrous or finely papillose; at anthesis reflexed, ca. 4 mm long, elliptic. Stamens 9, all 4-celled, the cells lateral, filaments of the outer 6 stamens dorsally pubescent; glands at base of inner stamens strongly enlarged and separating the outer stamens from each other; bases of filaments fused into a pubescent column, ca. 1 mm long. Ovary slender, glabrous, gradually narrowed into the style; inside of the floral tube and column formed by the stamens densely pubescent. Fruit unknown. Flowers: July and December. Elevation range: 600–1,400 m.

*Collections studied.* COLOMBIA. ANTIOQUIA: Amalfi, Salazary Marengo, *Callejas 9143* (MO). ECUADOR. LOS RIOS: Centinela Ridge, *van der Werff et al. 12365* (AAU, B, BR, C, COL, E, F, G, GH, HBG, K, KUN, LE, MEXU, MO, NY, QCNE, QRS, S, SEL, U, US), *van der Werff et al. 12367* (AAU, QRS, MO, QCNE). PICHINCHA: Cima de las Montañas de Ila, *Dodson 14531* (MO).

*Pleurothyrium tomiwahlii* is readily identified by its clustered, obovate leaves, long petioles with swollen base, its flowers with reflexed tepals, and the base of the filaments united in a column, giving the flower the appearance of a gonoloboid Asclepiadaceae species. Its closest relatives are the Costa Rican *P. golfodulcense*, in which the androecium

FIGURE 42. *P. tomiwahlii.* — A. Habit. — B, C. Flower sideways and seen from above. — D. Part of inflorescence. — E. Leaf base. — F. Shade leaf, showing less obovate shape and more acute leaf base.

forms a dome (without a column) and in which the glands separate the outer stamens just as in *P. tomiwahlii*; and the Panamanian species *P. racemosum* and *P. pilosum*, with similar floral structure as in *P. golfodulcense*, and with relatively long petioles, obtuse leaf bases and apices, and clustered leaves as in *P. tomiwahlii*. Details of indument, leaf shape and size as mentioned in the species descriptions, as well as the reflexed tepals, characterize *P. tomiwahlii*.

There is considerable variation in leaf size among the few available collections, probably a result of exposure to sunlight. The type tree, with rather small leaves, was free-standing in a pasture, while *van der Werff et al. 12367* was an understory tree in a forest patch. The Dodson collection has the largest leaves and was growing in forest. *Pleurothyrium tomiwahlii* is a rare species; during a day-long search at Centinela only three individuals were seen. Although the single Colombian collection represents a great range extension, *P. tomiwahlii* is such a distinctive species that I have no doubt about its identification.

The specific epithet honors the Wahl family, in recognition of their keen interest in conservation of tropical forests.

**Pleurothyrium trianae** (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra trianae* Mez, Jahrb. Bot. Gart. Berlin 5: 439. 1889. TYPE: Colombia. *Triana 1037* (holotype, P not seen; isotypes, BM, NY). Figure 43.

*Pleurothyrium zulianense* Lasser, Bol. Tecn. Minist. Agric. 3: 18. 1942. *Octoea zulianense* (Lasser) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Venezuela. Zulia: en selvas claras del Río Lora, *Pittier 10947* (holotype, VEN not seen; isotypes, G, GH, US).

*Pleurothyrium reflexum* Lasser, Bol. Tecn. Minist. Agric. 3: 18. 1942. *Ocotea reflexa* (Lasser) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Venezuela. Lara: entre San Isidro y Guarico, *Tamayo 1094* (holotype, VEN not seen; isotypes, F, US).

Large trees, becoming more than 20 m tall. Twigs roundly angular or terete, solid (rarely fistulose), glabrous, but the tips minutely brown-tomentellous, ca. 3 mm diam. 5 cm below the apex. Terminal buds minutely brown-tomentellous. Leaves alternate, chartaceous, elliptic, 9–25 × 3–10 cm, the upper surface glabrous, the lower surface minutely papillose to glabrous, the base acute, the tip shortly acuminate. Lateral veins 8–12 on each side, arching upward near the margin, not loop-connected, venation immersed on upper surface, midrib and lateral veins raised on lower surface. Petioles 10–20 mm long, shallowly canaliculate. Inflorescences in axils of cataphylls, minutely brown-tomentellous, paniculate, the branchlets once or twice cymosely branched, bracts deciduous at anthesis. Pedicels 2.5–4.5 mm long, minutely brown-tomentellous. Flowers white, ca. 4 mm diam., the tepals at anthesis erect or halfway spreading. Tepals 6, equal, ca. 2 mm long, the margin reflexed, minutely tomentellous outside, papillose inside. Stamens 9, glabrous, 4-celled, the cells mostly lateral and opening upward; filaments about as long as the anther, glands enlarged, visible as large lobes between the outer stamens, free. Ovary ellipsoid, glabrous or slightly papillose near the tip, style papillose, pistil 1.5–2.0 mm long. Receptacle glabrous inside. Cupule warty, to 15 mm wide, 10 mm tall, the pedicel not thickened; fruit ellipsoid, to 22 × 16 mm. Fruits: February–June. Flowers: collected in every month except June–July. Elevation range: 10–1,400 m.

*Collections studied.* COLOMBIA: *Triana 1037* (BM, NY). ANTIOQUIA: Frontino, Murri, 20–28 km from Nutibara, *McPherson 12999* (MO). CHOCO: Quebrada Taparal, hoya del Río San Juan, *Forero 4135* (MO); Taparalito, Quebrada Taparal, N of Palestina, *Gentry 53812* (MO), *Gentry 53833* (MO); Palo Gordo, *Triana 2042* (K); basin of Río San Juan, tributary Río Taparal, *van Rooden 650* (MO, U), *van Rooden 681* (MO, U); hoya del Río San Juan, Río Bicordo, arriba de Noanama, *Forero 4693* (MO); Quibdo, Río Cabi, *Prance 28012* (NY). NORTE DE SANTANDER: Sarare, Río Cubugon, junto a la quebrada de Gibraltar, *Cuatrecasas 13227* (F, US). VALLE: Río Calima, La Trojita, *Cuatrecasas 16321* (F, US), *Cuatrecasas 16321A* (F, U, US), *Cuatrecasas 16781* (F, US); lower Río Calima near junction with Río San Juan, *Gentry 53758* (MO); Río Calima, *Cuatrecasas 16675* (F), *Cuatrecasas 16864* (F, US). COSTA RICA. ALAJUELA: San Carlos, Refugio Cano Negro, Los Chiles, *Zamora 1363* (MO). PUNTARENAS: Osa, Reserva Florestal Golfo Dulce, *Hammel 18152* (MO). ECUADOR. LOS RIOS: Río Palenque Biological Center, *Dodson 6419* (MO). MORONA-SANTIAGO: Pozo Petrolero "Garza" de TENNECO, *Zak 4608* (MO). NAPO: Reserva Florestica El Ahuano, Estación INIAP, *Palacios 2094* (MO); 3 km from entrance to Jatun Sacha toward Río Arajuno, *Palacios 2804* (MO); Archidona, S slope of Sumaco, Comunidad El Pacto, *Palacios 4727* (MO); Tena, Estación Biológica Jatun Sacha, *Ceron 7416* (MO), *Palacios 4273* (MO), *Palacios 4334* (MO), *Palacios 4436* (MO, QCNE). HONDURAS. ATLANTIDA: Refugio Nacional de Vida Silvestre, *Soto 613* (MO). NICARAGUA: along Río San Juan, *Bunting 872* (F, NY, US). PERU. LORETO: Maynas, Indiana, Explorama Reserve, *Vásquez 12921* (MO). VENEZUELA. Ticoporo Forest Reserve, *Breteler 3517* (NY, U, US); El Vigia, *Mocquerys 1002* (K, NY, U). BARINAS: banks of Río Bumbun, *Aristeguieta 1584* (NY, VEN); near Ciudad Bolivia (Pedraza), *Aristeguieta 1647* (NY, VEN); Reserva Forestal de Ticoporo, *Aristeguieta 6978* (VEN); Pedraza La Vieja, Río Pedraza, *Bernardi 1137* (G, MO); Ticoporo Forest Reserve, bank of Río Bumbun, *Breteler 3667* (NY, US); Distr. Pedraza, *Dorr 4720* (MO, NY, PORT); Reserva Forestal de Caparo, *Jimenez 1289* (NY), *Marcano 2913*

FIGURE 43. Distribution of *P. trianae* (★) and *P. williamsii* (●).

(BR, G, MO); Caserio Barragan, *Salcedo 225* (G, US); Cacao, Barinitas, *Valverde 15* (MO). LARA: *Tamayo 1094* (F, US); Iribarren, Parque Nacional Terepaima, Fila San Esteban, *Smith 7463* (MO); Iribarren, Parque Nacional Terepaima, Represa Río Claro, *Smith 9021* (MO); Iribarren, Loma de los Naranjos, Montana de Macanillal, *Steyermark 111580* (G, NY, U, VEN). MERIDA: *Little 15822* (NY), *Marcano 1177* (MO). PORTUGUESA: Guanare, 17 km NW of Tucupido, N slope of Fila Las Palmas, *Davidse 21459* (MO, NY), *Davidse 21467* (MO, NY). PORTUGUESA/BARINAS: Represa de Bocono, *Aymard 1747* (MO). TACHIRA: La Fria, *Little 16121* (VEN). TRUJILLO: Carretera Campo Elias-Bocono, *van der Werff 8887* (MO). ZULIA: near Mission de Tukukos, Perija, *Aristeguieta 2085* (NY); road Machiques–Colon, near Río Caratumbo, *de Bruijn 1422* (MO, NY, US, VEN); along Río Lora, above Camp 2, Perija, *Pittier 10947* (G, GH, US).

*Pleurothyrium trianae* is, as treated here, a wide-ranging and variable species. It has been recorded from Honduras to Ecuador and Venezuela, but the records are not evenly distributed over this area. Only two collections are known from Central America. Nearly all South American collections come from the following three areas = (a) Pacific lowlands of Colombia (type locality of *P. trianae*), (b) Andean foothills in Venezuela (type localities of *P. zulianense* and *P. reflexum*), and (c) the Oriente of Ecuador, while almost no collections are known from the intervening areas. It is therefore not surprising to find local differentiation. The Colombian collections tend to have almost glabrous leaves, a rather sparse indument on twigs, and pedicels that are 3.5–4.5 mm long. The Venezuelan plants have more indument on twigs and leaves and have pedicels 2–2.5 mm long. The Ecuadorian plants agree with the Colombian specimens in their indument, have variable length of pedicels (2–4 mm), and have smaller leaves (9–14 × 3–5 cm) than the other populations (*Palacios 2094* has larger leaves). These differences are nearly all quantitative and form an insufficient basis for the recognition of separate taxa. The length of pedicels cannot be relied on for the separation of taxa because the lateral flowers of a cyme nearly always have shorter pedicels than the central flower and young flowers tend to have slightly shorter pedicels than old flow-

ers. I expect that once collections of *P. trianae* become available from other areas, the differences between populations as described above will disappear. For example, a collection from Antioquia at 1,050 m elevation (*McPherson 12999*) has the denser indument and shorter pedicels commonly found in Venezuelan collections; it also has stiffer leaves than usual for *P. trianae*.

The relationships of *P. trianae* are with a small group of poorly defined species that is characterized by small flowers with erect, more or less inrolled tepals, solid twigs, and chartaceous leaves. This group consists of *P. acuminatum*, *P. amapaense*, *P. amplifolium*, *P. intermedium*, and *P. undulatum*. *Pleurothyrium acuminatum* differs in its relatively long pedicels ((4–)5(–8) mm), and long tepals (3 mm long); *P. amplifolium* has broad leaves, while *P. intermedium*, *P. undulatum*, and *P. amapaense* have a different indument. It is possible that, once more material is available, some of these species will be placed in synonymy.

More distantly related are *P. parviflorum* and *P. poeppigii*, which both have fistulose twigs. Additionally, *P. parviflorum* differs in its glabrous flowers and *P. poeppigii* in its coriaceous leaves. A few collections of *P. trianae* have fistulose stems, and the differences cited above help separate these specimens from *P. parviflorum* and *P. poeppigii*. Differences between *P. trianae* and *P. cuneifolium* are discussed under the latter species.

**Pleurothyrium undulatum** (Meissner) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 44. 1986. *Oreodaphne undulata* Meissner, DC. Prodr. 15(1): 115. 1864. *Ocotea undulata* (Meissner) Mez, Jahrb. Bot. Gart. Berlin 5: 278. 1889. TYPE: Brazil. Amazonas: Prov. Rio Negro, *Riedel 1412* (holotype, LE not seen; isotypes, B, G, K, L, NY). Figure 41.

Tree of unknown size. Twigs terete, solid, minutely brown-tomentellous, glabrescent with age. Terminal bud brown-tomentellous. Leaves alternate, chartaceous, elliptic to narrowly elliptic, 10–17 × 2–5 cm, base and tip acute, glabrous on upper surface, glabrous or minutely papillose on lower surface, venation immersed on upper surface, midrib raised on lower surface, the lateral veins (12–15 on each side) poorly visible and less elevated; marginal vein poorly developed or lacking. Petioles ca. 1.5 cm long, with similar pubescence as twigs. Inflorescences in axils of cataphylls or leaves, brown-tomentellous, especially the ultimate branches, 8–12 cm long, paniculate, the branchlets 2–3 times cymosely branched, the flowers close together; bracts present, ovate, to 2 mm long, tomentellous outside, minutely so inside. Pedicels to 1 mm long, tomentellous. Flowers ca. 3 mm diam., the tepals ± erect at anthesis. Tepals 6, equal, ca. 2 mm long, tomentellous outside, papillose inside, the margin reflexed. Stamens 9, 4-celled, the cells lateral, glands enlarged and protruding between the outer stamens, but not enclosing them and not fused. Ovary globose, glabrous, enclosed by the glabrous receptacle; style papillose. Fruits unknown.

*Collection studied.* BRAZIL. *Riedel 1412* (B, G, K, L, NY).

*Pleurothyrium undulatum* is only known from the type collection made by Riedel in 1824–1825. Meissner (1864) gave as locality only Amazonas, Prov. Rio Negro; the isotype in NY gives as locality Barra, an old name for Manaus. *Pleurothyrium undulatum* was placed by Mez (1889) in *Ocotea*; he considered that the presence of glands at the base of all stamens was typical for *Pleurothyrium*, and although he noted that in respect of anther shape this species resembled *Pleurothyrium*, he treated it in *Ocotea* because of the presence of only six glands. *Pleurothyrium undulatum* belongs to a small group of species characterized by tepals with reflexed margins, often erect tepals at anthesis, marginal vein lacking or weakly developed, small flowers (less than 5 mm diam.) and inflorescences sometimes present in axils of leaves and not restricted to axils of cataphylls. Within this group, the narrow, almost glabrous leaves and the tomentellous pubescence of the inflorescences characterize this species.

**Pleurothyrium vasquezii** van der Werff, sp. nov. TYPE: Peru. Loreto: Maynas, km 32 along carretera Iquitos-Nauta, elev. 150 m, primary forest, *Vasquez & Jaramillo 7889* (holotype, MO; isotypes, AAU, AMAZ, F, G, NY). Figures 44, 45.

Arbor, 20 m alta. Ramuli teretes, solidi, fusco-tomentosi. Folia alterna, firme chartacea vel coriacea, elliptica vel late elliptica, 15–30 × 5–10 cm, basi acuta vel obtusa (rotundata), apice acuminata, supra glabra, subtus pilis erectis praedita, venatione supra immersa, subtus elevata, in dimidio distali brochydodroma, venis lateralibus 9–13 utroque costae latere. Petioli 1.5–3 cm longi, canaliculati. Inflorescentiae ex bractearum axillis ortae (raro ex foliorum axillis), fusco-tomentosae, 10–17 cm longae, paniculatae. Pedicelli 3 4 mm longi. Flores 5–6 mm diametro, rotati. Tepala 6, aequalia, oblonga, ca. 2 mm longa, margine plano, extus tomentella, intus papillosa. Tubus floralis ad ostium constrictus. Stamina 9, 4-locellata, locellis lateralibus vel extrorso-lateralibus, minute papillosa; glandulis magnis, staminibus exterioribus cingentibus, libe-

FIGURE 44. Distribution of *P. vasquezii* (★).

ris. Ovarium ellipticum, papillosum, ca. 1 mm longum, in receptaculo profundo, papilloso inclusum. Cupula verrucosa, 1 cm alta, 1.3 cm lata.

Tree, to 20 m tall. Twigs solid, terete, fuscous-tomentose, glabrescent, 3–4 mm diam. 5 cm below the tip. Terminal bud fuscous-tomentose. Leaves alternate, stiffly chartaceous to coriaceous, elliptic to broadly elliptic, 15–30 × 5–10 cm, the base acute to obtuse, rarely rounded, the tip shortly acuminate, the upper surface glabrous and with immersed midrib and lateral veins, the lower surface with erect hairs, the surface well visible, the elevated midrib and, to a lesser degree, lateral veins tomentose, tertiary venation also raised, lateral veins 9–13 on each side, curving upward near the margin, a marginal vein quite well developed in the distal half. Petioles 1.5–3 cm long, canaliculate, with same kind of tomentum as twig. Inflorescences in axils of cataphylls, rarely in axils of leaves, fuscous-tomentose, 10–17 cm long, paniculate, the branchlets 2–3 times cymosely branched, many-flowered, bracts lacking at anthesis. Pedicels 3–4 mm long, tomentose. Flowers yellow or green, 5–6 mm diam., the tepals spreading at anthesis. Tepals 6, equal, oblong, ca. 2 mm long, the margin plane, tomentellous outside, papillose inside. Floral tube constricted just below tepals. Stamens 9, 4-celled, the cells lateral or one pair lateral-extrorse, opening back-to-back, filaments and anthers minutely papillose; glands enlarged, almost completely enclosing the outer stamens, but not fused. Ovary elliptic, papillose, ca. 1 mm long, enclosed in the papillose, deep receptacle, the upper part covered by the enlarged glands, style ca. 0.5 mm long, papillose; stigma not enlarged, partly hidden by the longer stamens. Cupule cup-shaped, warty, ca. 1 cm tall, 1.3 cm wide (but probably not fully mature). Fruits: February. Flowers: August–October. Elevation range: 100–600 m.

*Collections studied.* BRAZIL. ACRE: Rio Jurua, 1 km upstream from Colonia Rodrigues Alvez, *Campbell 10852* (MO, NY); Reserva INCRA Santa Luzia, km 40 BR-364,

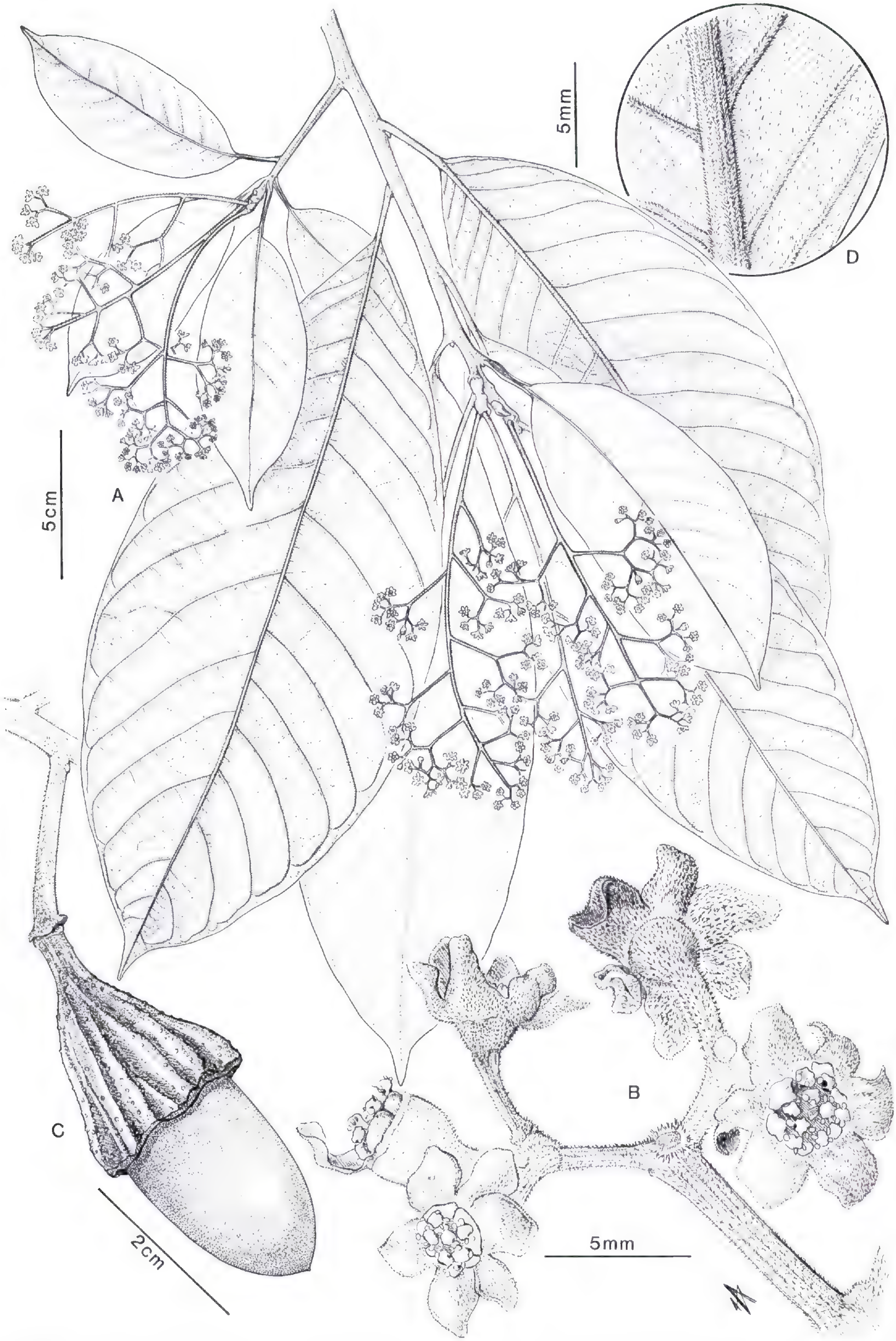



FIGURE 45. *P. vasquezii.*—A. Habit.—B. Part of inflorescence with flowers.—C. Fruit.—D. Detail of lower leaf surface.

*Campbell 6887* (MO, NY). AMAZONAS: Mun. de Itapiranga, Rio Uatuma, *Cid 859* (MO, NY); Manaus, *Froes 20526* (NY, US); Rio Negro, Vaupes, Jauarete, *Froes 21235* (NY); Rio Negro, Rio Jauapari, Estirão Tacuera, *Santos 78* (NY). RONDONIA: Mun. Porto Velho, Usina Hidroelectrica Samuel, *Thomas 6476* (MO, NY). PERU. LORETO: Maynas, Alpahuayo, *Grandez 1376* (MO); Maynas, Mishana, halfway between Iquitos and Sta. Maria de Nanay, *Ramirez 61* (HBG, MO); Pto. Almendras, *Vásquez & Jaramillo 5469* (MO); Maynas, Carretera Iquitos–Nauta, km 32, *Vásquez & Jaramillo 7889* (AAU, AMAZ, F, G, MO, NY); Requena, Arboretum Jenaro Herrera, without data (MO). MADRE DE DIOS: 39 km SW of Puerto Maldonado, *Smith & Jaramillo 384* (MO, US); Manu, Parque Nacional Manu, Rio Sotileja, *Foster 11719* (MO); Tambopata, Tambopata Nature Reserve, *Gentry 58103* (MO). SAN MARTIN: Mariscal Caceres, Tocache Nuevo, Quebrada de Mantención, *Schunke 13643* (MO); Mariscal Caceres, Distr. Campanillo, near Caserio de Sion, *Schunke 3475* (F). UCAYALI: Coronel Portillo, Bosque Nacional Alexander von Humboldt, *Oliveira 21* (MO).

*Pleurothyrium vasquezii* is known from several collections in Amazonian Peru and adjacent Brazil, as far downstream as Manaus. It is the only *Pleurothyrium* species in this area with a sparse, erect pubescence on the lower leaf surface and alternate leaves. *Pleurothyrium brochidodromum* has a very similar indument on the lower leaf surface, but differs in having larger flowers (9–10 vs. 5–6 mm diam.) and in its clustered leaves. A few collections placed in *P. vasquezii* were earlier identified as *P. panurense* (Allen, 1964), but this species has clustered leaves, a very short, appressed indument on the lower leaf surface that completely covers the surface, and flowers ca. 8 mm in diameter.

Two Froes collections (*20526, 21235*) from Brazil have somewhat more coriaceous leaves and roundish leaf bases. However, these collections are fruiting, which may explain their stiffer leaf texture. Because *Ramirez 61* from Peru also has roundish leaf bases and agrees in floral characters with *P. vasquezii*, I placed the Brazilian collections here. Spichiger et al. (1989) reported this species as *Nectandra amplifolia* Mez (= *P. amplifolium* (Mez) Rohwer) from the Arboretum at Jenaro Herrera, Peru (tree 159 in parcela 1). This latter species differs in its puberulous indument on the lower leaf surface, and in its more or less erect tepals with reflexed margins. The same tree is also cited under *Ocotea undulata* (Meissner) Mez (= *P. undulatum* (Meissner) Rohwer), which also has a different indument on the lower leaf surface, and more or less erect tepals with reflexed margins at anthesis.

*Pleurothyrium vasquezii* is named after Rodolfo Vasquez, whose fine collections have added much to our knowledge of the trees in Amazonian Peru.

**Pleurothyrium westphalii** van der Werff, Ann. Missouri Bot. Gard. 74: 410. 1987. TYPE: Guatemala. Alta Verapaz: Sacté, *Kunkel 9* (holotype, BR). Figures 41, 46.

Tree, to 20 m tall. Twigs solid, terete, young ones with brown, dense appressed pubescence, older ones glabrous. Terminal bud densely brown-pubescent. Leaves alternate, membraneous, 15–20 × 4–7 cm, elliptic or narrowly elliptic, the base acute, the margin somewhat decurrent, apex acute, glabrous and gland dotted on the upper surface (except for some appressed hairs near the base of the midrib), lower surface with few appressed hairs, more so near the base; lateral veins 5–9 on each side, arching upward near the margin, but not loop-connected; venation immersed on upper surface, midrib, lateral veins and tertiary venation weakly raised on lower surface. Petioles to 1 cm long, with similar pubescence as twigs. Inflorescences in axils of deciduous bracts, attached below the leaves, ca. 8 cm long, densely gray-brown pubescent, the lowest branches once cymosely branched, otherwise inflorescence racemose. Flowers ca. 8 mm diam. Pedicels ca. 4 mm long. Tepals 6, equal, ovate, 3–4 mm long, densely pubescent on both surfaces. Stamens 9, 4-celled, the cells lateral, anthers glabrous, filaments brown-pubescent; glands strongly enlarged, completely enclosing outer stamens; ovary ellipsoid, glabrous, ca. 1 mm long, enclosed by the glabrous receptacle; stigma platelike. Fruits unknown. Flowers: April. Elevation range: 900–1,100 m.

*Collections studied.* GUATEMALA. ALTA VERAPAZ: Sacte, *Kunkel 9* (BR), *Kunkel 17* (MO).

*Pleurothyrium westphalii*, known only from two collections in Guatemala, is the northernmost representative of the genus. The species can be readily identified by its appressed, gray-brown pubescence, the pubescent tepals (also inner surface is pubescent), pubescent filaments, the few-flowered inflorescences, the membraneous leaves, and the absence of a marginal vein.

**Pleurothyrium williamsii** O. C. Schmidt, Repert, Spec. Nov. Regni Veg. 31: 189. 1933. *Ocotea williamsii* (O. C. Schmidt) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Peru. Loreto: Pebas on the Amazon River, *Llewelyn Williams 1766* (holotype, F probably lost; isotype, B, fragment G). Figure 43.

Shrub or small tree, to 8 m tall. Twigs angular, solid, becoming terete in age, brown-tomentellous to glabrous, 4–5 mm diam. 5 cm below apex.

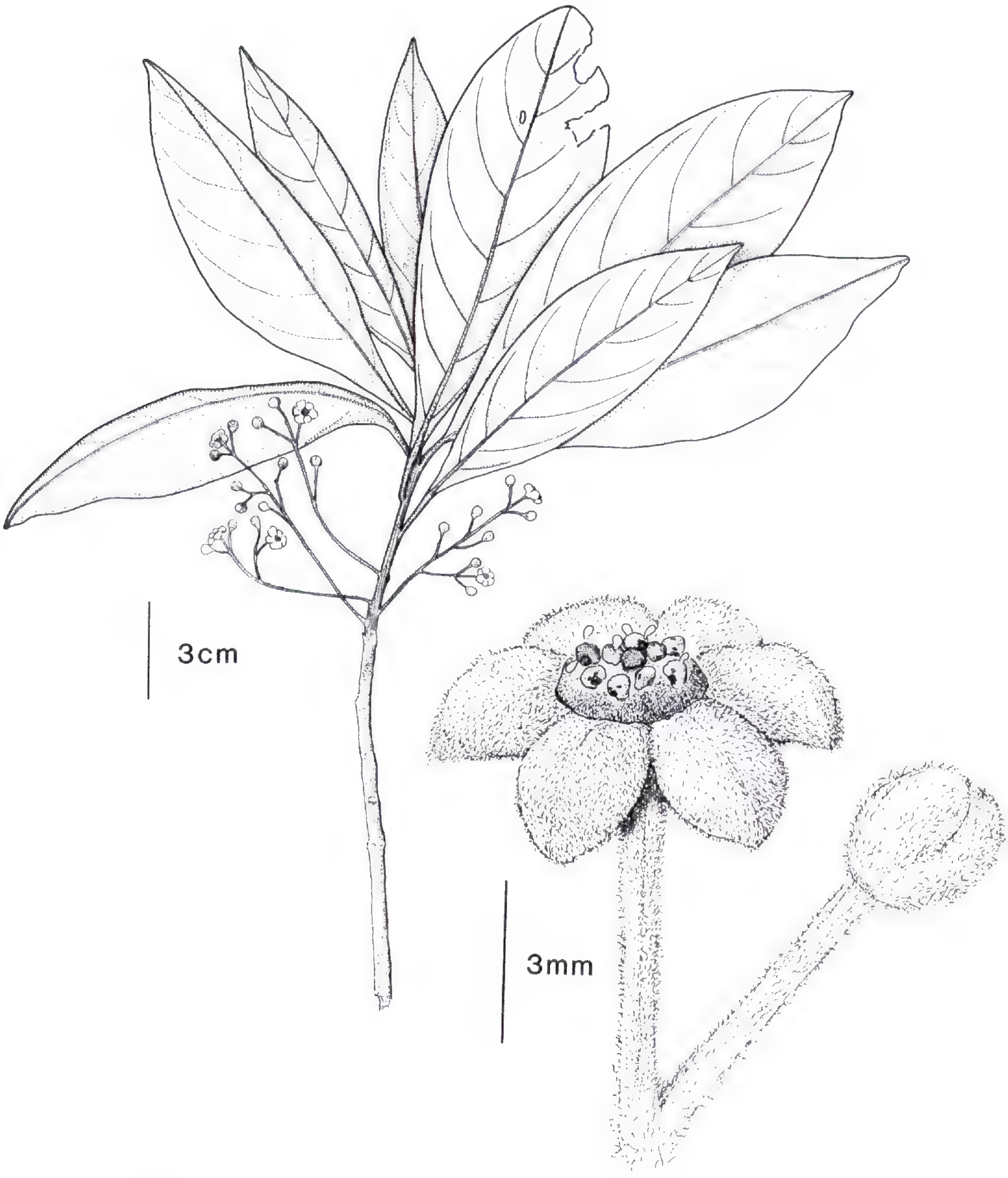



FIGURE 46. *P. westphalii*. Habit and flower.

Leaves clustered, rarely alternate, chartaceous, 30–40 × 6–11 cm, oblanceolate or narrowly obovate, the base cordate, the tip acuminate, acumen to 3 cm long, both surfaces glabrous, but with varying amounts of minute hairs on midrib and lateral veins; venation immersed on upper surface, midrib and lateral veins raised on lower surface, the tertiary venation weakly raised; lateral veins 20 25 on each side, curving upward near the margin and prominently loop-connected in the upper ⅔ of the lamina. Petioles to 8 mm long, with similar indument as twig. Inflorescences in axils of deciduous bracts, pendent, to 20 cm long, rufous-tomentellous, the branchlets 2–3 times cymosely branched, bracts present at anthesis, ovate, tomentellous, to 4 mm long. Flowers white, 8–9 mm diam. Pedicels 3 mm long. Tepals 6, subequal, the outer three slightly wider than the inner three, the outer three tomentellous outside, inner three with a basal triangular tomentellous patch, otherwise papillose, inside of all tepals papillose. Stamens 9, 4-celled, the cells lateral, anthers minutely papillose, glands

of stamens greatly enlarged, surrounding the stamens, fused. Ovary and style densely brown-papillose, floral tube brown-papillose inside; ovary globose, ca. 0.7 mm long, the style distinct, ca. 0.5 mm long. Cupule of young fruit cup-shaped, ca. 2 cm wide and 1 cm tall; young fruit ellipsoid, ca. 1.5 cm long. Fruits: July–October. Flowers: June–July.

*Collections studied.* ECUADOR. NAPO: Aguarico, Reserva Faunistica Cuyabeno, *Palacios 7667* (MO). PERU. LORETO: Quebrada Sucursari, tributary of Río Napo, *Gentry 54300* (MO); Pebas on the Amazon River, *Williams 1766* (B); Maynas, Iquitos, Asociación Agraria Paujil, *Vásquez 10877* (MO); Maynas, Explornapo Camp, Río Sucursari, *Vásquez 8119* (MO), *Vásquez 13078* (MO).

*Pleurothyrium williamsii* is only known from the type collection, four collections, all from Peru in the area north of the Río Napo–Río Amazonas, and one collection from Ecuador. Unfortunately, the holotype, which was requested from the Field Museum, disappeared, together with other *Pleurothyrium* types, while being sent to St. Louis. Of the type collection, only a duplicate in B (with buds) and some inflorescence fragments in G (with a few flowers) exist. The recent collections are a good match as far as floral characters and leaf shape are concerned, but there are some differences. The B specimen has alternate leaves, while the recent specimens and the photo of the holotype (in NY and F) show clustered leaves. The phototypes have the inflorescences alternate along a leafless twig, the recent specimens have the inflorescences near the tip of the stem, while the B specimen has a detached inflorescence. The B specimen is also more tomentulose. However, the similarities in leaf shape and flowers outweigh these differences, and I do not hesitate to assign the two recent collections to *P. williamsii*.

A close relative of this species is *Pleurothyrium panurense* (Meissner) Mez, a species with elliptic-obovate leaves, an obtuse leaf base and similar flowers. It differs, however, in its smaller leaves, the whitish indument on the lower leaf surface, its glabrous ovary, and longer petioles. *Pleurothyrium insigne* differs from *P. williamsii* in its larger leaves, the leaves not so gradually narrowed toward the base, erect indument on lower leaf surface, and its larger flowers. All three species occur in Amazonian Peru and/or adjacent Brazil. Another close relative is *P. maximum*, which see for further discussion.

## IMPERFECTLY KNOWN SPECIES

Among the collections were found a number of specimens that do not belong to any of the treated species and which very likely represent undescribed species. Because these specimens are incomplete (sterile or fruiting), they are not formally described, but only listed below so as to call attention to their existence. I hope that in the near future material adequate for their description will become available.

*G. Proctor Cooper 539*, Panama, Bocas del Toro, region of Almirante (F, NY, US).

A fruiting collection with large (to 35 cm), elliptic to elliptic-oblong, acuminate leaves. Leaves are glabrous below and have a strongly developed marginal vein; the twigs are solid, glabrous or nearly so. A distinct species, included in Burger & van der Werff (1990) as *Pleurothyrium* sp. A.

*Gentry 57004*, Colombia, Valle, Bajo Calima (MO).

A sterile specimen with gigantic leaves, according to the label ca. 1 m long. The specimen has leaves 60–70 cm long and 30–35 cm wide, densely rusty-tomentose below.

*Monsalve 1651*, Colombia, Valle, Bajo Calima (MO).

A species with clustered leaves, dark ferruginous-tomentose below, ca. 15 × 6 cm. Young inflorescences and infructescences are very short, ca. 1 cm long, and carry only one bud or fruit. There are five collections of this species, but none with flowers.

*López & H. Triana 24*, Colombia, Antioquia, Parque Nacional de las Orquideas (MO).

Characterized by its obovate to obovate-elliptic leaves, glabrous below, with 15–20 pairs of lateral veins and an obtuse to rounded leaf base. The young cupules are covered with many small lenticels.

*Vasquez 3220*, Peru, Loreto, Requena (MO).

Leaves glabrous, whorled, narrowly oblong with abruptly rounded base. Related to *P. williamsii*, but with narrower, oblong leaves and much smaller inflorescences.

## EXCLUDED SPECIES

*Pleurothyrium bahiense* (Meissner) Barroso = *Urbanodendron bahiense* (Meissner) Rohwer

*Pleurothyrium chrysothyrsus* Meissner = *Rhodostemonodaphne*

*Pleurothyrium cowanianum* C. K. Allen = *Rhodostemonodaphne kunthiana* (Nees) Rohwer

*Pleurothyrium ferrugineum* Meissner = *Ocotea arnottiana* (Nees) van der Werff
*Pleurothyrium glandulosum* (Lundell) Lundell = *Nectandra*
*Pleurothyrium velutinum* Meissner = *Ocotea calophylla* Mez

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List of species recognized. New species are in boldface.

1. **Pleurothyrium acuminatum** van der Werff
2. *Pleurothyrium amapaense* Allen
3. *Pleurothyrium amplifolium* (Mez) Rohwer
4. *Pleurothyrium bifidum* Nees
5. **Pleurothyrium bracteatum** van der Werff
6. **Pleurothyrium brochidodromum** van der Werff
7. **Pleurothyrium cinereum** van der Werff
8. *Pleurothyrium costanense* van der Werff
9. **Pleurothyrium crassitepalum** van der Werff
10. *Pleurothyrium cuneifolium* Nees
11. **Pleurothyrium giganthum** van der Werff
12. **Pleurothyrium glabrifolium** van der Werff
13. **Pleurothyrium glabritepalum** van der Werff
14. *Pleurothyrium golfodulcense* Burger & Zamora
15. *Pleurothyrium grandiflorum* van der Werff
16. *Pleurothyrium hexaglandulosum* van der Werff
17. **Pleurothyrium insigne** van der Werff
18. *Pleurothyrium intermedium* (Mez) Rohwer
19. **Pleurothyrium marginale** van der Werff
20. *Pleurothyrium maximum* O. C. Schmidt
21. *Pleurothyrium nobile* A. C. Smith
22. **Pleurothyrium obovatum** van der Werff
23. *Pleurothyrium palmanum* (Mez & J. D. Smith) Rohwer
24. *Pleurothyrium panurense* (Meissner) Mez
25. *Pleurothyrium parviflorum* Ducke
26. **Pleurothyrium pauciflorum** van der Werff & Hammel

27. **Pleurothyrium pilosum** van der Werff
28. *Pleurothyrium poeppigii* Nees
29. **Pleurothyrium prancei** van der Werff
30. **Pleurothyrium racemosum** van der Werff
31. *Pleurothyrium steyermarkianum* Allen
32. **Pleurothyrium synandrum** van der Werff
33. **Pleurothyrium tomentellum** van der Werff
34. **Pleurothyrium tomiwahlii** van der Werff
35. *Pleurothyrium trianae* (Mez) Rohwer
36. *Pleurothyrium undulatum* (Meissner) Rohwer
37. **Pleurothyrium vasquezii** van der Werff
38. *Pleurothyrium westphalii* van der Werff
39. *Pleurothyrium williamsii* O. C. Schmidt

*Specimens studied.* If collected by a team, only last name of the first collector on the label is listed. Thus, Berg & Akkermans becomes Berg.

*Allen 5885* (14); *Ancuash 602* (4); *Aristeguieta 1584* (35); *Aristeguieta 1647* (35); *Aristeguieta 2085* (35); *Aristeguieta 6978* (35); *Ayala 574* (10); *Ayala 3386* (35); *Ayala 5734* (24); *Aymard 1747* (35).

*Barbour 1011* (23); *Berg 1050* (25); *Bernardi 1137* (35); *Bernardi 2169* (31); *Bernardi 6879* (8); *Bosque J-03* (8); *Bosque J-03A* (8); *Bosque J-12* (8); *Brandbyge 42343* (22); *Brandbyge 42366* (22); *Breteler 3517* (35); *Breteler 3667* (35); *Bunting 872* (35); *Burger 4690* (14).

*Callejas 9143* (34); *Campbell 6887* (37); *Campbell 10852* (37); *Campos 364* (10); *Cardenas 3966* (28); *Castillo 12* (21); *Castillo 15* (21); *Castillo 50* (1); *Ceron 3017* (12); *Ceron 4982* (25); *Cid 859* (37); *Cid Ferreira 7292* (25); *Cogollo 170* (10); *Croat 17593* (25); *Croat 19439* (17); *Croat 59792* (16); *Cuatrecasas 13227* (35); *Cuatrecasas 13986* (9); *Cuatrecasas 16321A* (35); *Cuatrecasas 16656* (32); *Cuatrecasas 16675* (35); *Cuatrecasas 16781* (35); *Cuatrecasas 16864* (35); *Cuatrecasas 17196* (19).

*Davidse 21459* (35); *Davidse 21467* (35); *Davidse 27524* (2); *Davidson 5336* (17); *de Bruijn 1422* (35); *de Nevers 7520* (27); *Díaz 241* (25); *Dodson 6302* (11); *Dodson 6419* (35); *Dodson 10181* (11); *Dodson 13632* (11); *Dodson 14531* (34); *Dorr 4720* (35); *Ducke RB19935* (25); *Ducke RB25676* (1).

*Forero 4135* (35); *Forero 4693* (35); *Foster 3153* (28); *Foster 10642* (28); *Foster 11719* (37); *Freitas 55* (25); *Froes 20526* (37); *Froes 21036* (25); *Froes 21235* (37).

*Gentry 7201* (13); *Gentry 16627* (25); *Gentry 18317* (25); *Gentry 21284* (25); *Gentry 25807* (25); *Gentry 25914* (25); *Gentry 28959* (25); *Gentry 39902* (10); *Gentry 43560* (28); *Gentry 45117* (7); *Gentry 45760* (10); *Gentry 53812* (35); *Gentry 53833* (35); *Gentry 54300* (39); *Gentry 57817* (10); *Gentry 58103* (37); *Gentry 58574* (10); *Glaziou 17731* (3); *González 1215* (8); *Grandez 1376* (37); *Grandez 1732* (25); *Gudiño 12* (33); *Gudiño 17* (33).

*Haber 9526* (23); *Hammel 14781* (16); *Hammel 17009* (26); *Hammel 17909* (26); *Hammel 18152* (35); *Hartshorn 2631* (10); *Hartshorn 2937* (10); *Huber 1557* (10); *Hurtado 1464* (33).

*Janse 280* (7); *Jativa 1104* (7); *Jativa 2039* (7); *Jimenez 648* (14); *Jimenez 1289* (35); *Juncosa 1675* (15).

*Kayap 145* (10); *Kayap 648* (10); *Kernan 184* (14); *Kernan 187* (14); *Klug 1301* (25); *Klug 1372* (25); *Klug 2122* (7); *Klug 2779* (10); *Klug 2931* (10); *Klug 3116* (10); *Klug 3195* (10); *Klug 3228* (10); *Klug 3567* (10); *Knapp 8205* (17); *Kroll 285* (21); *Kroll 422* (21); *Krukoff 4783* (24); *Krukoff 4800* (24); *Krukoff 5121* (21); *Krukoff 5255* (28); *Krukoff 5263* (28); *Krukoff 5722* (28); *Krukoff 6232* (17); *Kunkel 9* (38); *Kunkel 17* (38).

*Lamotte 085* (25); *Lamotte 0200* (25); *Lau 10* (8); *Lawrance 619* (5); *Lawrance 780* (10); *Little 8488* (10); *Little 15822* (35); *Little 16121* (35); *Little 21359* (7); *Llewelyn Williams 1090* (25); *Llewelyn Williams 2273* (25); *López 8634* (25); *Lugo 320* (28).

*Marcano Berti 1123* (8); *Marcano Berti 1177* (35); *Marcano Berti 2913* (35); *Matthews 1432* (10); *McDaniel 15243* (25); *McDaniel 20716* (25); *McDaniel 20753* (25); *McPherson 12120* (30); *McPherson 12999* (35); *McPherson 13365* (10); *Miranda Bastos 17* (25); *Mocquerys 1002* (35); *Mori 9074* (25); *Mori 9227* (25); *Mori 20470* (25).

*Neill 6555* (28); *Neill 7019* (10); *Neill 7128* (10); *Neill 7603* (28); *Neill 8741* (33); *Neill 8783* (33); *Neill 8954* (7); *Neill 9033* (17); *Neill 9435* (18); *Neill 9439* (18); *Nuñez 5901* (28); *Nuñez 12207* (10).

*Oliveira 21* (37); *Ortiz 192* (22).

*Palacios 982* (28); *Palacios 1332* (17); *Palacios 1518* (17); *Palacios 2094* (35); *Palacios 2288* (12); *Palacios 2775* (28); *Palacios 2804* (35); *Palacios 3416* (33); *Palacios 4273* (35); *Palacios 4334* (35); *Palacios 4388* (17); *Palacios 4436* (35); *Palacios 4727* (35); *Palacios 7667* (39); *Pariona 49* (17); *Pariona 63* (10); *Peters 52/84* (25); *Pires 51430* (2); *Pittier 10947* (35); *Plowman 6410* (25); *Plowman 6908* (25); *Poeppig* Addenda *301* (28); *Poeppig 1718* (10); *Poeppig 1845* (10); *Poeppig 2125* (10); *Poeppig 2398* (4); *Poeppig 2908* (10); *Prance 11970* (25); *Prance 12392* (29); *Prance 13927* (24); *Prance 28012* (35).

*Quintero 11* (8).

*Ramírez 61* (37); *Riedel 1412* (36); *Revilla 742* (25); *Revilla 2532* (25); *Revilla 3687* (24); *Reynel 102* (10); *van Rooden 650* (35); *van Rooden 681* (35); *Rowlee 233* (23); *Rubio 45* (33); *Ruíz 1438* (25); *Ruíz s.n* (28).

*Salcedo 225* (35); *Santos 78* (37); *Schunke 3475* (37); *Schunke 13643* (37); *Shepherd 537* (10); *Smith 384* (37); *Smith 1743* (10); *Smith 1756* (10); *Smith 2793* (28); *Smith 3061* (10); *Smith 7463* (35); *Smith 9021* (35); *Soejarto 1268* (28); *Soto 613* (35); *Soukop 910* (10); *Spruce 2449* (24); *Stern 1064* (23); *Steyermark 56077* (31); *Steyermark 61393* (8); *Steyermark 62230* (8); *Steyermark 96072* (8); *Steyermark 111580* (35).

*Tamayo 1094* (35); *Tessmann 4040* (20); *Tessmann 4529* (20); *Tessmann 4634* (7); *Tessmann 5175* (25); *Thomas 6476* (37); *Tonduz CR 12652* (23); *Triana 1037* (35); *Triana 2042* (35).

*Ule 9408* (18); *Unknown s.n.* (37).

*Valverde 15* (35); *Vásquez 896* (35); *Vásquez 1520* (25); *Vásquez 4858* (25); *Vásquez 4970* (24); *Vásquez 5469* (37); *Vásquez 7468* (24); *Vásquez 7823* (17); *Vásquez 7865* (6); *Vásquez 7889* (37); *Vásquez 8119* (39); *Vásquez 8444* (17); *Vásquez 9138* (25); *Vásquez 9365* (17); *Vásquez 10233* (24); *Vásquez 10500* (25); *Vásquez 10877* (39); *Vásquez 11507* (25); *Vásquez 12284* (25); *Vásquez 12921* (35); *Vásquez 13078* (39).

*Wallnoefer 18-29788* (33); *van der Werff 3654* (8); *van der Werff 8266* (10); *van der Werff 8287* (10); *van der Werff 8291* (10); *van der Werff 8343* (28); *van der Werff 8345* (28); *van der Werff 8346* (10); *van der*

*Werff 8673* (10); *van der Werff 8887* (35); *van der Werff 9471* (11); *van der Werff 9956* (25); *van der Werff 9967* (1); *van der Werff 10050* (25); *van der Werff 10066* (25); *van der Werff 11157* (10); *van der Werff 12362* (11); *van der Werff 12365* 934); *van der Werff 12367* (34); *Whitford 49* (8); *Williams 1090* (25); *Williams 1766* (39); *Williams 2273* (25); *Williams 2715* (10); *Wurdack 2047* (4).

*Zak 4459* (33); *Zak 4511* (17); *Zak 4608* (35); *Zamora 1363* (35).

Note added in proof.

At the very last moment, the collection *Herrera & Fallas 4638* was received for identification. This collection represents an undescribed species, which could not be incorporated in the manuscript. The description of this species and a discussion of its affinities are presented in this note.

**Pleurothyrium immersum** van der Werff, sp. nov. TYPE: Costa Rica. Punarenas: Cantón de Golfito, Dos Brazos de Río Tigre, Fila Puriscal Rico (fls), *Herrera & Fallas 4638* (holotype, MO; isotypes, BM, CR, HBG, INB, MEXU, QRS, US, USJ).

Haec species *P. golfodulcense* proxima, sed foliis floribusque minoribus, reticulatione immersa, tepalis intus pubescentibus et inflorescentia paniculato-cymosa differt.

Tree, 20 m tall. Twigs terete, solid, finely gray appressed-pubescent, 1–2 mm diam. ca. 5 cm below the tip. Terminal bud densely appressed-pubescent. Leaves alternate, firmly chartaceous, 5–9 × 1.5–2.5 cm, elliptic, base acute, tip acuminate or acute, upper surface glabrous, gland dotted, lower surface with scattered appressed hairs, these more dense along midrib, or glabrous; midrib slightly raised on both surfaces, otherwise venation immersed and scarcely visible; lateral veins 5 6, not loop-connected. Petioles 4 9 mm long, finely appressed-pubescent. Inflorescences in axils of normal leaves or cataphylls, paniculate-cymose, the lateral branchlets once or twice cymosely branched, densely gray-pubescent, bracts often present at anthesis, narrowly elliptic, to 1.5 mm long, pubescent on both surfaces. Flowers yellow-green, the tepals spreading to bent downward, ca. 5 mm diam. Pedicels 2–4 mm long. Tepals 6, equal or nearly so, pubescent on both surfaces, the margin plane, elliptic, ca. 2 mm long, the inner 3 ca. 1.5 mm wide, outer 3 ca. 1 mm wide. Stamens 9, all 4-celled, fully immersed in the glandular mass, with only the cells and valves recognizable; glands strongly enlarged, fused, and forming a pillowlike mass; stamens, especially those of whorl II, separated from each other by the glandular tissue and not restricted to the center of the glandular mass. Pistil ca. 1.2 mm long, the moderately pubescent ovary gradually narrowed into the glabrous style. Receptacle pubescent inside. Cupule and fruit unknown. Flowers: November. Elevation range: ca. 700 m.

*Pleurothyrium immersum* is only known from the type collection made on the Osa Peninsula, collected in the same general area as *P. golfodulcense*; these two species are closely related. Characters shared by both are the position of the stamens in the glandular mass (not crowded together in the center, but stamens of whorl II separated from the others by the glandular tissue), position of inflorescences (not infrequently in axils of normal leaves), the reflexed tepals in older flowers, and the acute-acuminate leaf tips. However, the two species differ in the following characters: *P. immersum* has much smaller leaves (5 9 vs. 10–20 cm), the lateral veins are immersed and not raised on lower leaf surface, flowers are much smaller (4–5 vs. 9–12 mm diam.), tepals are pubescent (not papillose) on inner surface, and the inflorescences are paniculate-cymose, not racemose.

In the key, *Pleurothyrium immersum* would run to couplet 37, where the combination in *P. immersum* of pubescent inner surface of tepals and a pubescent pistil will cause a problem. However, *P. immersum* differs from all other *Pleurothyrium* species with glabrous or appressed-pubescent lower leaf surfaces in its small leaves with immersed venation. The glandular dots on the upper leaf surface are also a good indicator for this species.

# A REVISION OF *PANICUM* SUBG. *DICHANTHELIUM* SECT. *DICHANTHELIUM* (POACEAE: PANICOIDEAE: PANICEAE) IN MESOAMERICA, THE WEST INDIES, AND SOUTH AMERICA[1]

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## Abstract

A revision of *Panicum* subg. *Dichanthelium* sect. *Dichanthelium* (Poaceae: Panicoideae: Paniceae) for Mesoamerica, the West Indies, and South America is presented, considering exomorphological, anatomical data and caryological characters. Thirty-seven species and seven varieties of section *Dichanthelium* of *Panicum* are recognized from this area. *Panicum caparaoense* is described as a new species, and *Panicum dichotomum* var. *tenue* as a new combination. An anatomical description of section *Dichanthelium*, with photomicrographs of representative species, is given, together with a key, morphological descriptions, and distribution maps. It is concluded that section *Dichanthelium* is not sufficiently distinct to be regarded as a separate genus. The taxonomic position of *Dichanthelium* within *Panicum* is discussed.

*Dichanthelium* was established by Hitchcock & Chase (1910) as a subgenus of *Panicum* in their treatment of North American species of the genus. *Dichanthelium* was delimited due to the presence of an overwintering rosette of short, broad leaves, which produce simple culms with terminal, chasmogamous inflorescences in the spring. Later in the season, branch culms arise at the nodes of the vernal culms, forming loose to rather dense fascicles of reduced leaves and branches together with cleistogamous inflorescences.

Hitchcock & Chase (1910) recognized 17 informal groups in *Dichanthelium*, 110 species and 5 subspecies. The taxa were distinguished principally by characters of the spikelet and leaf blade. Gould (1974) raised *Dichanthelium* to generic rank. This decision was followed by Clark & Gould (1975), Brown & Smith (1975), Gould & Clark (1978), Clark (1977), Gould (1980), Freckmann (1981a, b), and Hansen & Wunderlin (1988) based on the foliar and floral dimorphism, ploidy level, Kranz syndrome, and ornamentation of the upper anthecium as diagnostic characters for the genus. Pohl (1980), Lelong (1984), Zuloaga (1987), Webster (1988), and Morrone & Zuloaga (1991), however, retained *Dichanthelium* as a subgenus of *Panicum*, due to a lack of adequate characters to support the segregation of these two taxa. Variation in several characters, such as the presence or absence of the basal rosette, and foliar and floral dimorphism in tropical species were not considered by Hitchcock & Chase (1910), Gould (1974), and subsequent authors in their decision to separate *Dichanthelium* from *Panicum*.

The present treatment includes a comprehensive taxonomic and anatomical analysis of the 37 species of section *Dichanthelium* occurring in Mesoamerica, the West Indies, and South America, which comprise all tropical species of the section.

## Materials and Methods

Scanning electron micrographs (SEMs) were prepared of the upper anthecia of most of the species, utilizing the procedures described by Soderstrom & Zuloaga (1989). The vouchers for this

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study are marked with an asterisk in the specimens examined section of the taxonomic treatment. Field procedures included collection and drying of herbarium specimens, and immediately fixing leaves, spikelets, and other structures in FAA (formalin-ethanol-acetic acid) (Johansen, 1940) and thereafter transferring this material to 70% ethanol in the laboratory for storage. Transverse sections of leaf blade material 10 μm thick were prepared after desilicification in 30% hydrofluoric acid (Breakwell, 1914), dehydration in a methyl cellosolve series (Feder & O'Brien, 1968), and embedding in Tissue Prep (Fisher Scientific); the sections were stained in safranin and fast green.

Abaxial epidermal scrapes of leaf blades were prepared by removing the mesophyll and vascular tissue with a scalpel and camel hair brush following the method of Metcalfe (1960). The epidermis was stained in safranin.

The standardized terminology of Ellis (1976, 1979) was used to describe the anatomical structure of the leaf blades. The following abbreviations are used in the anatomical description:

vb/s—vascular bundle/s
1′vb/s—first-order vascular bundle/s
2′vb/s—second-order vascular bundle/s
3′vb/s—third-order vascular bundle/s
ibs—inner bundle sheath; i.e., mestome sheath
obs—outer bundle sheath; i.e., parenchyma sheath

## Morphology

*Basal rosette.* The rosette is typical of North American species of section *Dichanthelium* and is also sometimes present in some West Indian species, *P. scoparium* Lam., *P. aciculare* Desv., and *P. acuminatum* Sw. However, this feature is absent from species from Mesoamerica and South America, as well as from some species that are widespread in both North and South America, such as *P. aciculare*, *P. acuminatum*, and *P. sphaerocarpon* Elliott.

*Foliar dimorphism.* Leaf size is variable in representatives of section *Dichanthelium*. Leaf blades are usually broad and long on the main culms and smaller on the axillary culms in species from North America. However, this dimorphism is absent in species from Mesoamerica and South America. Main and axillary culms are persistent in Mesoamerican and South American species (Morrone & Zuloaga, 1991), while in North American species only the rosette usually persists.

*Inflorescences.* The inflorescence in section *Dichanthelium* is typically a lax, diffuse panicle borne on the uppermost node of the culm; it is short-exserted to exserted. The axes of the branches are pilose or glabrous; when glabrous they usually have multicellular glands. Each axis ends in a developed spikelet; these spikelets are solitary on the branches, or occasionally geminate in specimens of *P. hebotes* Trin. The panicle, although usually open, is contracted in *P. superatum* Hackel and *P. aciculare*.

*Glands.* Multicellular glands are a characteristic feature of several species of section *Dichanthelium*. These glands are present in *P. acuminatum*, *P. sabulorum* var. *polycladum* (E. Ekman) Palacios, *P. sabulorum* var. *cordatum* Zuloaga & Morrone, *P. stigmosum* Trin., *P. adenorachis* Zuloaga & Morrone, *P. sphaerocarpon*, *P. strigosum* Muhlenb., *P. surrectum* Chase ex Zuloaga & Morrone, *P. ensifolium* Elliott, *P. scoparium*, *P. cucaense* Zuloaga & Morrone, *P. divergens* HBK, and *P. laxiflorum* Lam. These glands occur on the axes of the inflorescence branches, peduncles, pedicels, culms, sheaths, and blades.

*Spikelets.* The spikelets are ellipsoid to obovoid, with two glumes, two florets, and two flowers. They disarticulate at the base of the lower glume. Lower glume length varies from ¼ to ⅘ the length of the spikelet. The upper glume and lower lemma are isomorphic and 7–11(–15)-nerved, or occasionally 5-nerved in *P. sciurotis* Trin. and *P. ensifolium*. The lower floret is either staminate or neuter; the lower palea may be as long as the lemma or reduced to absent in *P. aciculare* and *P. penicillatum* Nees ex Trin. The upper anthecium is almost as long as the spikelet; the upper lemma and palea are indurate, smooth and shining, and pale (but dark in *P. hebotes*) with simple papillae regularly distributed over the surface. The upper lemma is shortly apiculate or crested and pilose or glabrous, with the margins involute and covering ⅔ of the upper palea. The upper palea is 2-nerved. The upper floret is bisexual, with two conduplicately truncate lodicules that embrace the lower margins of the palea, three stamens, and a gynoecium with two free styles and a plumose stigma.

*Floral dimorphism.* Hitchcock & Chase (1910) and Gould & Clark (1978) described the presence of both chasmogamous and cleistogamous flowers in the species of *Dichanthelium* from North America. Study of herbarium specimens and native and cultivated Mesoamerican and South American plants, including widespread species from both North America and South America, demonstrated that the production of chasmogamous and cleistogamous flowers is extremely variable. Climatic fac-

tors, such as humidity and temperature, appear to determine the proportion of cleistogamous flowers produced.

Cleistogamous flowers also occasionally occur on species of section *Dichanthelium* from Mesoamerica and South America.

## Chromosome Numbers

Section *Dichanthelium* is characterized by a basic chromosome number of $x = 9$. Gould & Soderstrom (1967) mentioned one deviation in this character, a count of $2n = 20$, $x = 10$ for *P. missionum* Mez, non Ekman (= *Panicum surrectum* Chase ex Zuloaga & Morrone).

Most of the species are diploid, with $2n = 18$. In addition, six tetraploid counts, one hexaploid count, and one octoploid count are also known.

The following list summarizes chromosome counts determined for species of section *Dichanthelium* treated in the present contribution:

*Panicum aciculare* Desv. var. *aciculare*: $2n = 18$ (Brown, 1948; Dubcovsky & Zuloaga, 1992).

*P. aciculare* Desv. var. *arenicoloides* (Ashe) Beetle: $2n = 18$ (Brown, 1948; Gould, 1958; Burton, 1942, as *P. arenicoloides* Ashe; Brown, 1948, as *P. angustifolium* Elliot).

*P. acuminatum* Sw. var. *acuminatum*: $n = 9$ (Davidse & Pohl, 1972a, 1978, as *P. olivaceum* A. Hitchc. & Chase; Spellenberg, 1970, as *P. olivaceum*); $2n = 18$ (Dubcovsky & Zuloaga, 1992).

*P. acuminatum* Sw. var. *longiligulatum* (Nash) Lelong: $2n = 18$ (Brown, 1948, as *P. longiligulatum* Nash and *P. wrightianum* Scribner).

*P. aequivaginatum* Swallen: $2n = 18$ (Dubcovsky & Zuloaga, 1992).

*P. davidsei* Zuloaga & Morrone: $2n = 72$ (Dubcovsky & Zuloaga, 1992).

*P. dichotomum* L.: $2n = 18$ (Brown, 1948; Clark, 1977; Sherif et al., 1983; Brown, 1948, as *P. barbulatum* Michaux, *P. yadkinense* Ashe, and *P. caerulescens* Hackel ex A. Hitchc.).

*P. dichotomum* L. var. *unciphyllum* (Trin.) Zuloaga & Morrone: $2n = 18$ (Brown, 1948, as *P. albomarginatum* Nash).

*P. divergens* HBK: $2n = 18$ (Burton, 1942; Brown, 1948; Sherif et al., 1983, as *P. commutatum* Schult.).

*P. ensifolium* Baldwin ex Elliott: $2n = 18$ (Brown, 1948; Brown, 1948, as *P. chamaelonche* Trin.).

*P. laxiflorum* Lam.: $2n = 18$ (Brown, 1948; Gould, 1958; Pohl & Davidse, 1971; Bowden, 1960, as *P. xalapense* Kunth).

*P. portoricense* Desv. ex Ham.: $2n = 18$ (Brown, 1946; Brown, 1948, as *P. lancearium* Trin.).

*P. pycnoclados* Tutin: $2n = 18$ (Dubcovsky & Zuloaga, 1992).

*P. sabulorum* Lam. var. *polycladum* (E. Ekman) Palacios: $2n = 36$ (Parodi, 1946; Núñez, 1952, as *P. sabulorum*; Dubcovsky & Zuloaga, 1992).

*P. sabulorum* Lam. var. *sabulorum*: $2n = 54$ (Dubcovsky & Zuloaga, 1992; Parodi, 1946; Núñez, 1952, as *P. fultum* Hackel).

*P. sciurotoides* Zuloaga & Morrone: $2n = 18$ (Dubcovsky & Zuloaga, 1992).

*P. scoparium* Lam.: $n = 9$ (Davidse & Pohl, 1972b); $2n = 18$ (Brown, 1948).

*P. sphaerocarpon* Elliott: $n = 9$ (Spellenberg, 1970; Davidse & Pohl, 1972a, 1978; Reveal & Spellenberg, 1976); $2n = 18$ (Church, 1929; Brown, 1948; Gould, 1958; Pohl & Davidse, 1971; Reveal & Spellenberg, 1976; Dubcovsky & Zuloaga, 1992; Brown, 1948, as *P. sphaerocarpon* Elliott var. *inflatum* (Scribner & Smith) A. Hitchc.).

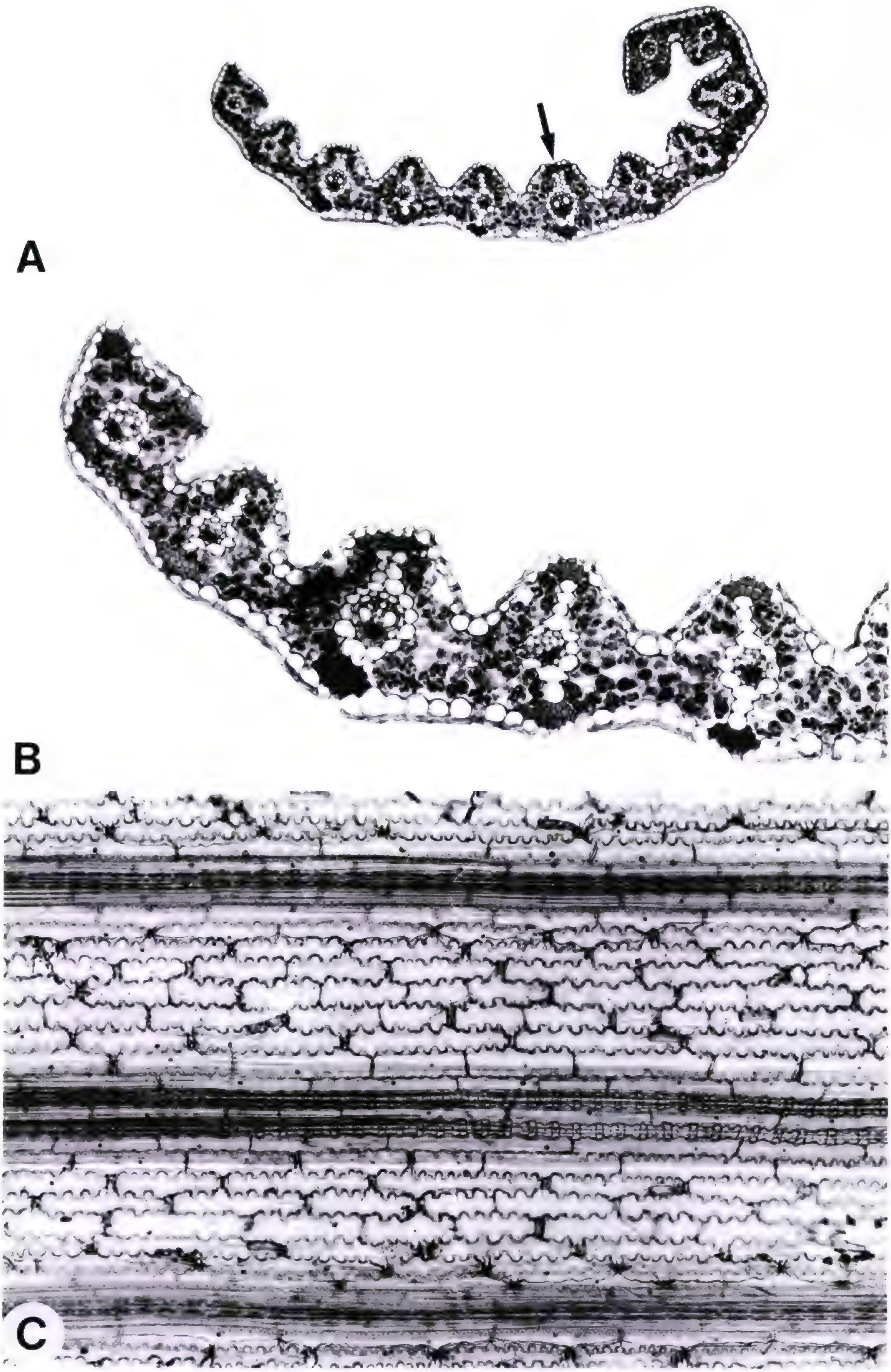
*P. strigosum* Muhlenb.: $2n = 18$ (Brown, 1946; Brown, 1948, as *P. ciliatum* Elliott).

*P. viscidellum* Scribner: $n = 18$ (Davidse & Pohl, 1972a, 1974); $2n = 36$ (Pohl & Davidse, 1971; Dubcovsky & Zuloaga, 1992).

## Leaf Anatomy

Anatomical data for 14 species of section *Dichanthelium* are presented by means of photomicrographs (Figs. 1–23). The following species were studied: *P. aciculare*, *P. acuminatum*, *P. aequivaginatum*, *P. cumbucana* Renvoize, *P. davidsei*, *P. hebotes*, *P. peristypum* Zuloaga & Morrone, *P. pycnoclados*, *P. sabulorum*, *P. sciurotoides*, *P. sphaerocarpon*, *P. stigmosum*, *P. superatum*, and *P. viscidellum*. For comparative purposes the North American species *P. boscii* Poir., *P. clandestinum* L., and *P. oligosanthes* Schultes are also included in this study. *Panicum acuminatum* is the only species studied anatomically with specimen samples from both American continents. For this species a comparison between the leaf anatomy of the basal rosette leaves and the cauline leaves is also made.

The leaf anatomy of section *Dichanthelium* is variable, with few unifying or diagnostic characters being evident; the vascular bundle sheaths and their extensions are the most consistent and valuable anatomical character for distinguishing the section


A
B
C

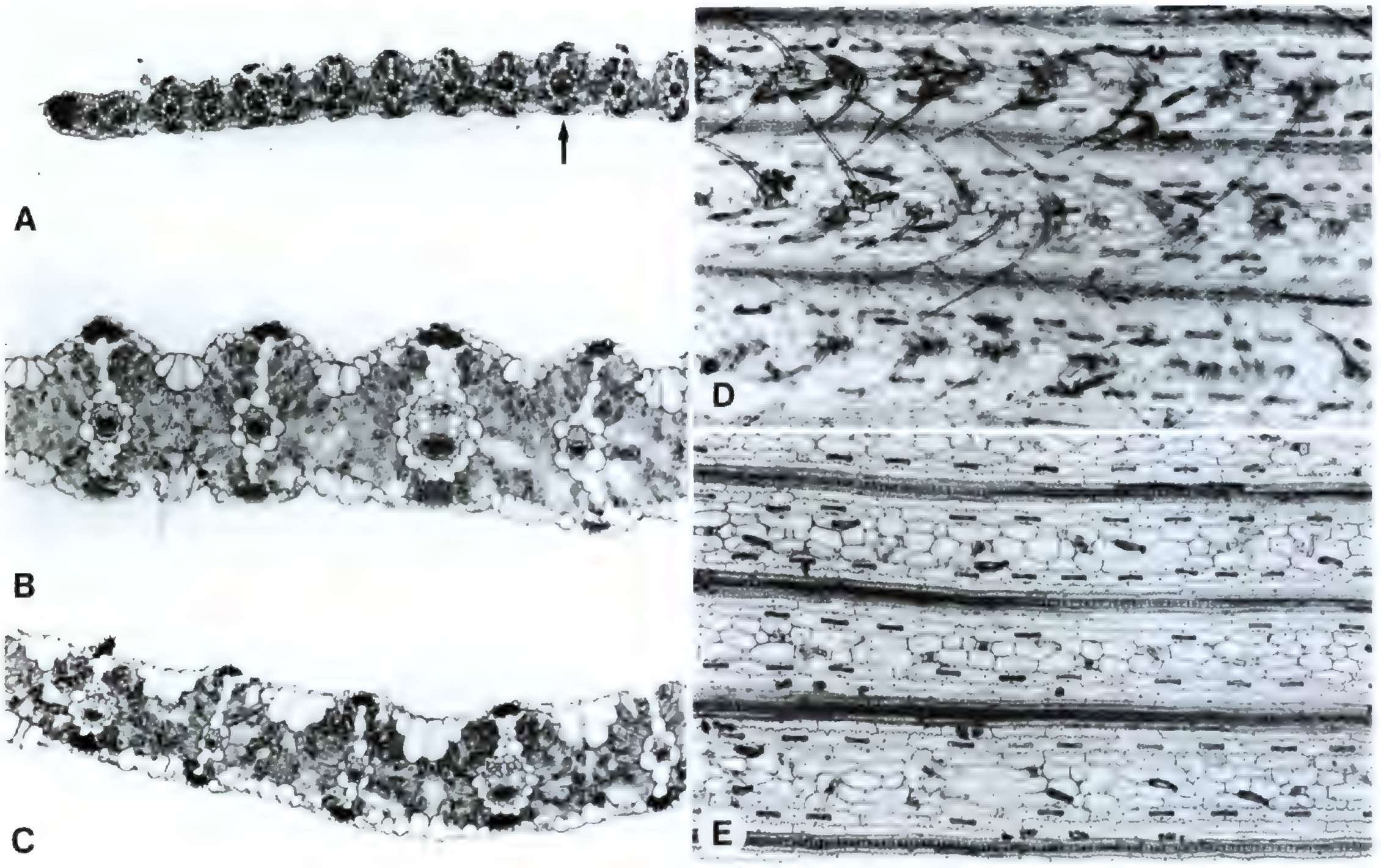



FIGURE 2. Leaf blade anatomy of South American specimens of *Panicum acuminatum*. A–C. Transectional anatomy.—A. Outline of half of lamina showing rounded margin with well-developed sclerenchyma cap and undifferentiated median vascular bundles (arrowed).—B. Detail of semiradiate chlorenchyma, colorless outer bundle sheath and extension cells, uniseriate adaxial and abaxial bundle sheath extensions, and small sclerenchyma strands associated with the third-order vascular bundles and slight adaxial ribs and furrows; note the raised cushion cells associated with the macrohairs, which are very common in the abaxial intercostal zones.—C. Specimen with thinner leaf without ribs and furrows. D, E. Abaxial epidermal structure.—D. Specimen with numerous recurved macrohairs located along the intercostal zones; microhairs also relatively common.—E. Specimen with few macrohairs, these associated with two inflated epidermal cells; the central files of the intercostal zones with bulliformlike long cells (based on *Zuloaga 4202*; A ×100; B–E ×250).

and subgenus *Dichanthelium* from most of the other $C_3$ subgenera of *Panicum*. A detailed description of section *Dichanthelium* based on the studied species is presented below.

## LEAF BLADE IN TRANSVERSE SECTION

*Outline:* expanded, either flat or very broadly V-shaped; arms of lamina either straight or outwardly bowed; two halves of lamina symmetrical about the median vascular bundle; leaf width variable and leaf blade section includes between 17 and 117 vbs; *P. aciculare* (Fig. 1) is an exception with narrow (only 11 vbs), inrolled leaf blades. *Ribs and furrows:* variable, from flat adaxial surfaces without ribs or furrows to medium furrows (about a quarter of the leaf thickness); furrows wide and open, occurring between all vbs; adaxial ribs, when present, located over the vbs, with rounded apices, and all are structurally uniform; abaxial ribs usually absent but slight ribbing may be developed; in *P. aciculare* abaxial ribs are clearly present (Fig. 1B). *Midrib:* variable, from undifferentiated median vb to definite keel; median vbs, structurally indistin-

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FIGURE 1. Leaf blade anatomy of *Panicum aciculare*. A. Blade outline showing atypical, narrow, slightly inrolled blade containing only three first-order bundles with the central median bundle (arrowed) structurally identical to the lateral first-order bundles.—B. Detail of unusually prominent adaxial ribs and furrows, small, bulliform cells, and thick abaxial cuticle without stomata; translucent parenchymatous sheath and extension cells are present as are adaxial and abaxial sclerenchyma strands; the rather dense mesophyll tissue exhibits no pattern of cellular arrangement.—C. Abaxial epidermis without stomata, the costal zones are five cells wide with cross-shaped silica bodies separated by tall and narrow cork cells, the intercostal long cells are elongated-rectangular with very sinuous walls, and small, narrow microhairs occur in the intercostal zones; macrohairs are absent (based on *Zuloaga & Londoño 4201*; A ×100; B, C ×250).

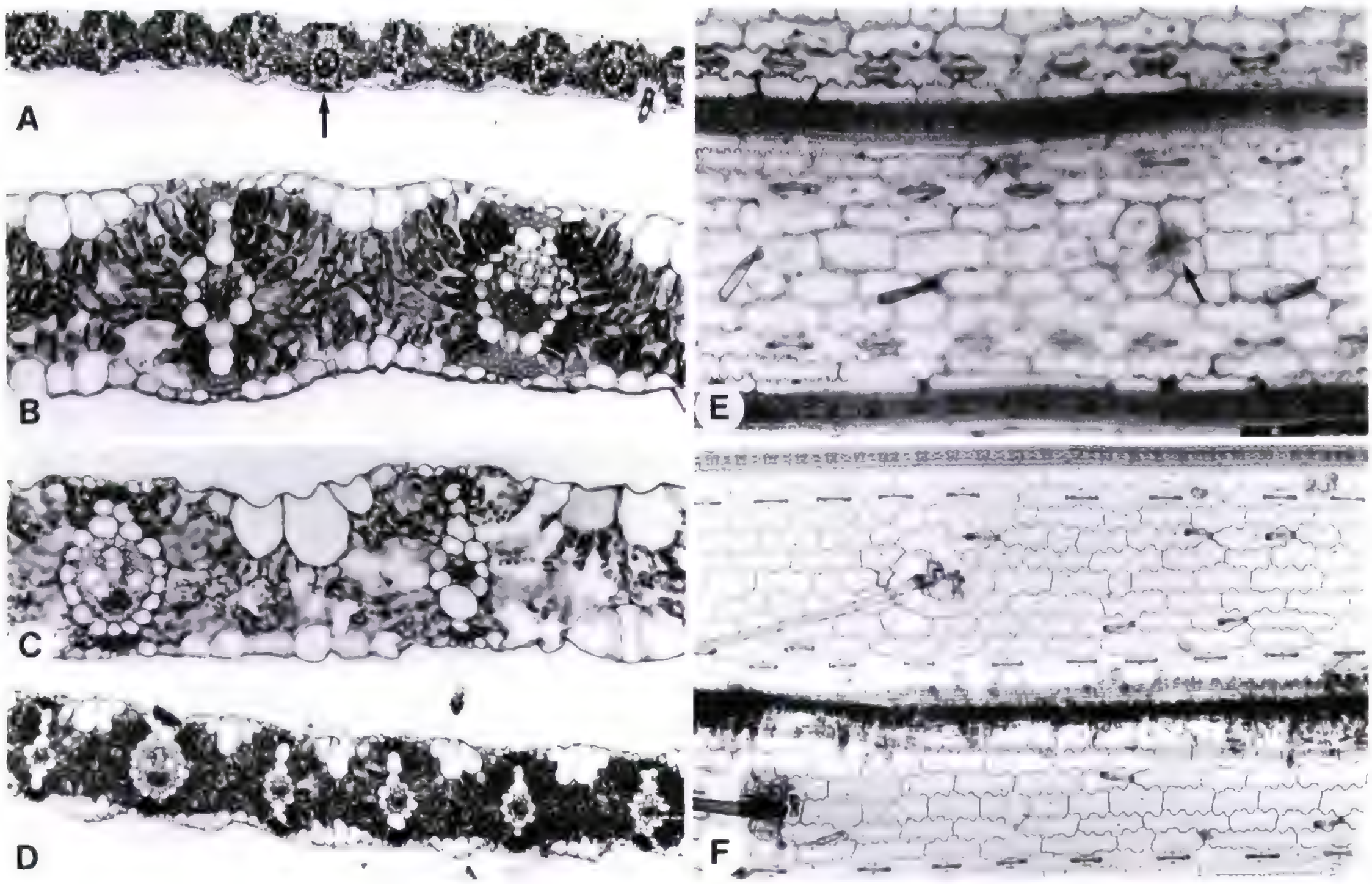


FIGURE 3. Leaf blade anatomy of *Panicum acuminatum* specimens from North America. A–D. Transverse leaf blade sections.—A. Median part of blade with midrib (arrowed) structurally barely distinct from lateral first-order bundles; note cushion-based macrohair; adaxial ribs and furrows not present.—B. Semiradiate chlorenchyma tissue with a tendency to adaxial palisade and abaxial spongy mesophyll tissue; note adaxial and abaxial uniseriate bundle sheath extensions associated with the third-order bundle, the extensions linked to small sclerenchyma strands.—C. Specimen with diffuse chlorenchyma tissue with very large intercellular air spaces and very thin cuticle. —D. Specimen with compact mesophyll tissue; no adaxial ribs or furrows developed. E, F. Abaxial epidermis.—E. Detail of small macrohair with associated cushion base cells (arrowed), elongated fingerlike microhairs (at least twice the length of the stomata), intercostal long cells and numerous stomata in files adjacent to the narrow costal zones.—F. Epidermis of specimen with thin cuticle and diffuse mesophyll; note macrohairs, sinuous walls of long cells, microhairs, stomata, and narrow costal zones, only three cells wide (A, B, E, based on *Davidse & Ellis 30825*; C, F, based on *Davidse & Ellis 30807*; D, based on *Zuloaga 2492*; A ×100; D, F ×250; B, C, E ×400).

guishable from other 1′vbs, most common (Figs. 2A, 5A, 12B, 15C, 16A, 17A, 18A, C, 23A); midribs (Figs. 3A, 11A, 14A, 21A) and keels (Figs. 8A, C, 10A, 22A) much less common; keels include either 1 or 3 abaxially positioned vbs and adaxially located parenchyma ground tissue; no lacunae present.

*Vascular bundle arrangement:* number of vbs very variable with 3, 5, 7, 9, 11, 13, or 15 1′vbs in entire blade; *P. aciculare*, with 3 (Fig. 1), and *P. sabulorum*, which may have only 5, also have the narrowest leaf blades; 2 (*P. aciculare* and *P. sabulorum*, Fig. 12D), 3, 4, 5, 6, 7, and rarely 8, 3′vbs are located between consecutive lateral 1′vbs; the wider the leaf the more 1′vbs and the more minor bundles are present between the 1′vbs; 2′vbs absent. Vbs usually displaced slightly toward the abaxial side of the blade thickness although they may be centrally situated; all vbs positioned at the same level. *Vascular bundle description:* 3′vbs angular with phloem distinguishable. 1′vbs elliptical in outline; phloem adjoins ibs; lysigenous cavities and protoxylem present; circular metaxylem vessels narrow with diameters less than half those of the obs cells. *Vascular bundle sheaths:* obs of 1′ and 3′vbs conspicuous, entire, round to elliptical, consisting of 5–8 (3′vbs) or 12–18 (1′vbs) inflated, rounded cells; chloroplasts absent except in a few specimens (e.g., *P. sphaerocarpon*, Fig. 15A–D, as well as specimens of *P. viscidellum* with silicified macrohair bases, Fig. 20). Adaxial and abaxial bundle sheath extensions in all species; adaxial 3′vb extensions usually uniseriate (but may be biseriate) and consisting of 1–5 cells, whereas abaxial extensions are shorter (usually only 1 cell deep) and wider; the extensions consist of conspicuous, thin-walled, colorless cells very similar to the obs cells; the extensions extend and join small

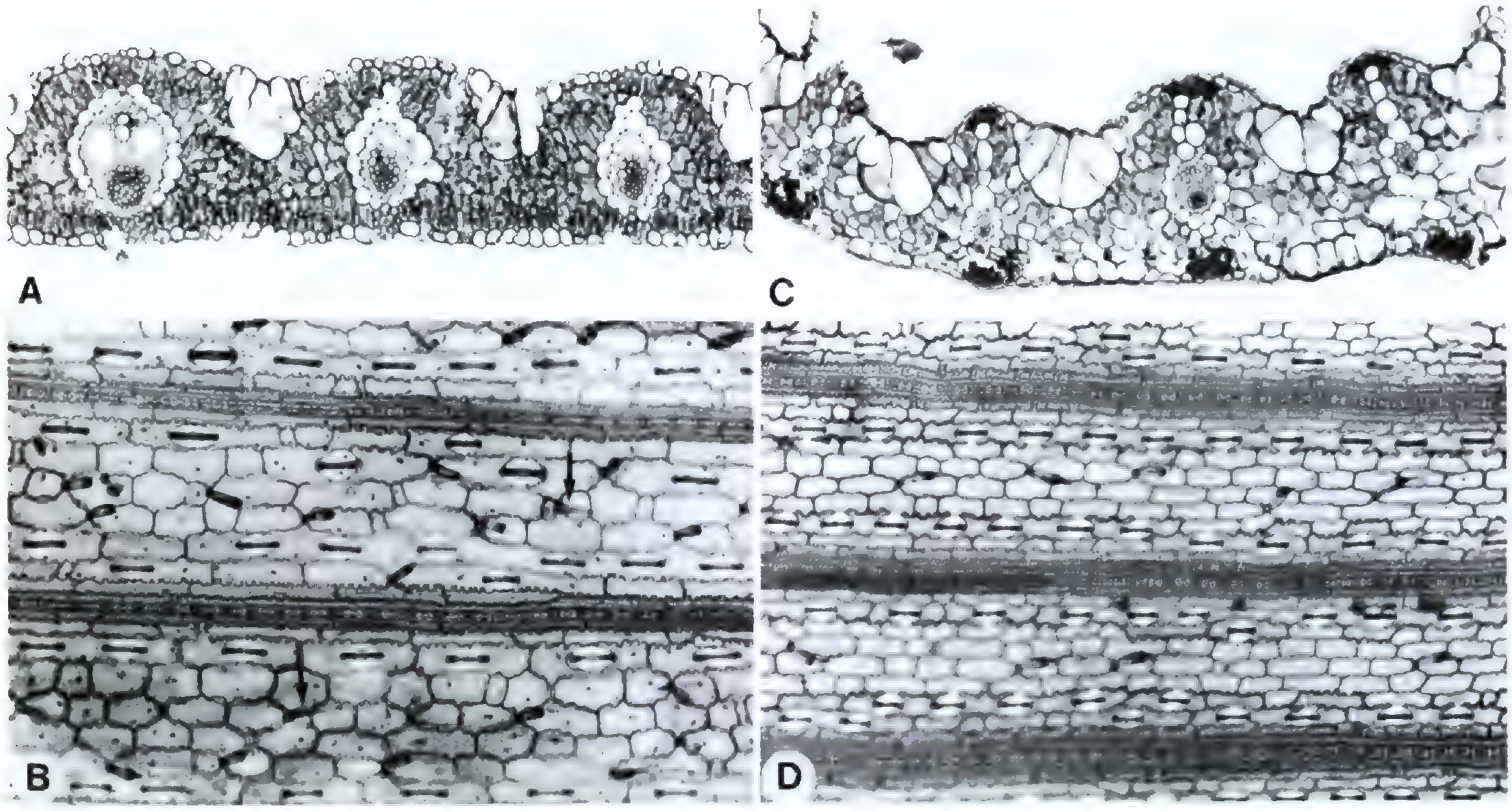


FIGURE 4. A comparison of the leaf blade anatomy of the upper culm leaves and the basal rosette leaves of *Panicum acuminatum*. A, B. Upper culm leaves.—A. Transverse section showing slight adaxial ribs and furrows, distinct bulliform cell groups, and very short bundle sheath extensions; the mesophyll is unusual in that the abaxially located cells are also palisadelike in their arrangement, and the mesophyll tissue is dense, without large intercellular air spaces.—B. Abaxial epidermis with short long cells, short microhairs (less than twice the length of the stomatal complexes) and dumbbell-shaped silica bodies alternating with cross-shaped cork cells on the central files of the costal zones; note the very short macrohairs (arrowed), these barely distinct from hooks except that they are associated with a single inflated epidermal cell. C, D. Basal rosette leaves.—C. Transverse section showing distinct adaxial ribs and furrows, well-developed uniseriate extensions to four cells long and diffuse mesophyll tissue with the abaxial cells resembling spongy mesophyll.—D. Abaxial epidermis with short long cells, microhairs at least twice the length of the stomata, no macrohairs, and with costal zones to five cells wide; the silica bodies are irregular in shape, often resembling the dumbbell type (A–D, based on *Zuloaga 2490*; A–D ×250).

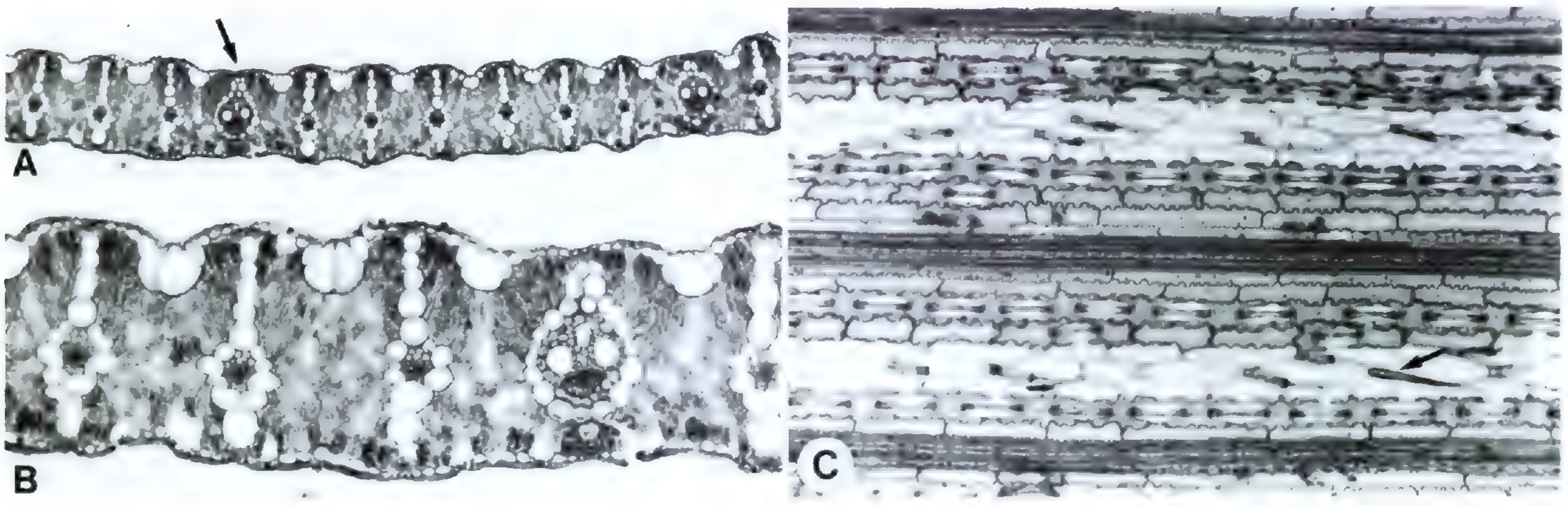


FIGURE 5. Leaf blade anatomy of *Panicum aequivaginatum*. A, B. Transectional anatomy.—A. Center of lamina showing median vascular bundle (arrowed) undifferentiated from other first-order vascular bundles.—B. Detail of conspicuous outer bundle sheath and uniseriate extension cells without chloroplasts; the mesophyll separable into spongy and palisade chlorenchyma tissue and the cells are densely arranged; bulliform cells are small and sclerenchyma strands minute.—C. Abaxial epidermis showing clear differentiation between the narrow costal zones with dumbbell-shaped silica bodies and much wider intercostal zones; the latter are differentially stained, the cell files adjacent to the costal zones as well as the interstomatal files staining darkly, the central files staining only slightly; microhairs and few short macrohairs (arrowed) are located along these central interstomatal files; specimens with thicker cuticles (e.g., B) lack these central intercostal files with microhairs and macrohairs (A, B, based on *Zuloaga et al. 4470*; C, based on *Zuloaga et al. 2469*; A ×100; B ×250; C ×400).

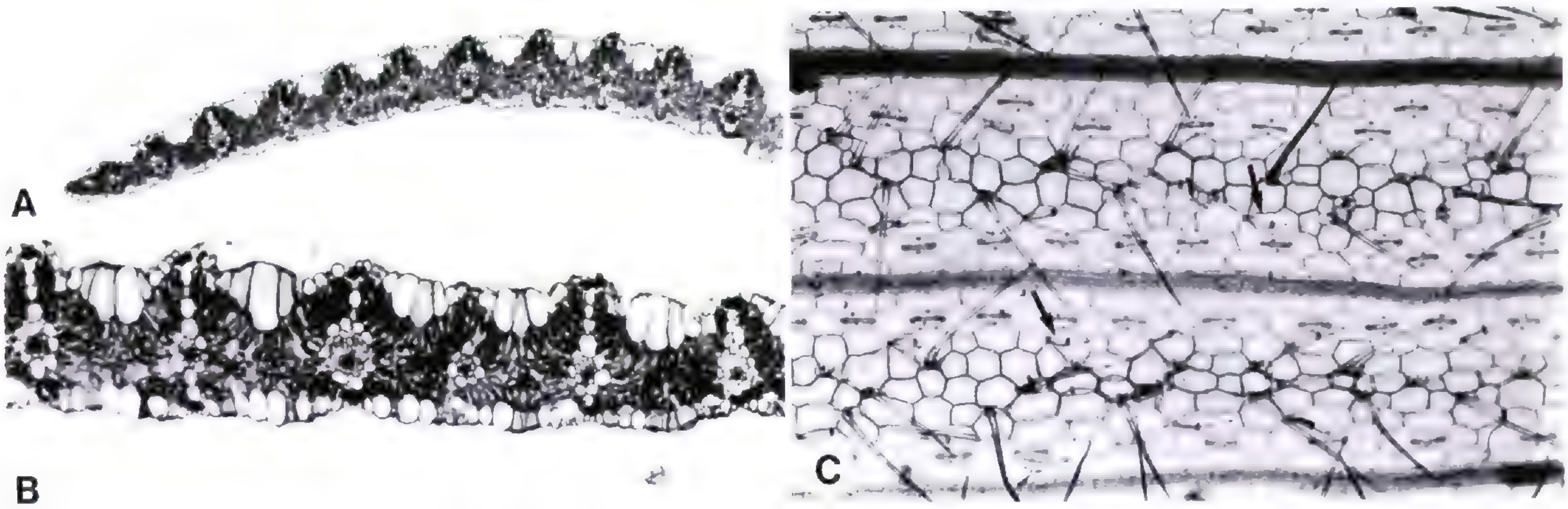


FIGURE 6. Leaf blade anatomy of *Panicum cumbucana*. A, B. Transverse leaf sections.—A. Gently tapering margin with evenly spaced vascular bundles.—B. Detail showing bundle sheath extensions, small adaxial and abaxial sclerenchyma strands and rather dense chlorenchyma tissue with a tendency toward the radiate type of cellular arrangement.—C. Abaxial epidermis structure with narrow costal zones only three to five cells wide; silica bodies are dumbbell-shaped to nodular and very narrow; the wide intercostal zones composed of short, hexagonal long cells and microhairs (arrowed) and macrohairs are common, the latter being rather short and pointed and inserted between only a few (two to three) specialized epidermal cells, one of which appears to be inflated (A–C, based on *Calderón 2425*; A ×100; B, C ×250).

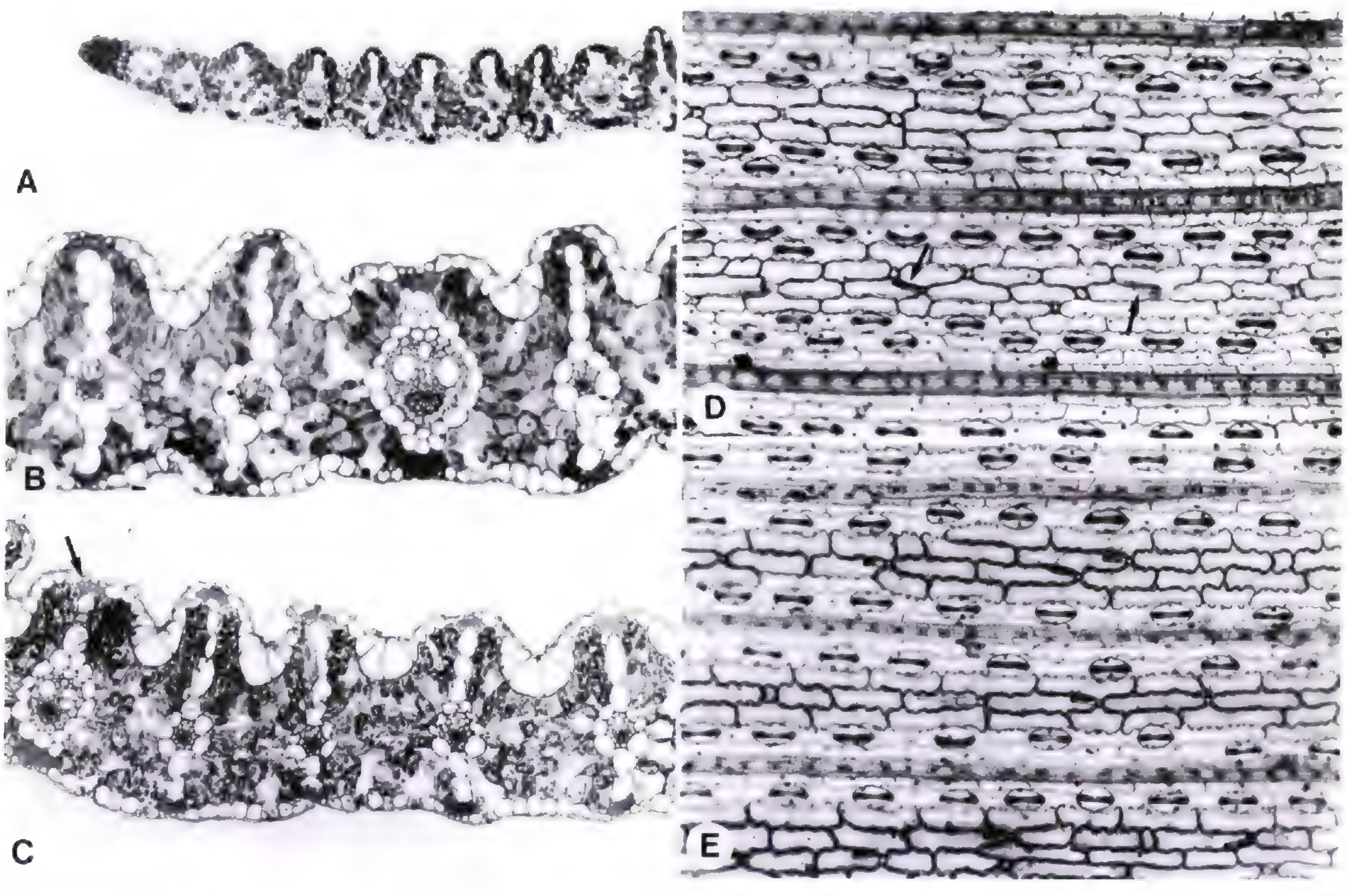


FIGURE 7. Leaf blade anatomy of *Panicum davidsei*. A–C. Transectional anatomy.—A. Gently tapering margin with sclerenchyma cap; adaxial ribs and furrows well developed, slight abaxial furrows present.—B. Long (four or more cells), uniseriate bundle sheath extensions associated with third-order bundles only—first-order bundles with wider extensions (triseriate) but much shorter, consisting of only one cell row; parenchyma sheath and extension cells conspicuous, translucent; the mesophyll approaches the radiate type, particularly the adaxial palisadelike tissue; bulliform cells small; small sclerenchyma strands associated with all bundles, both adaxially and abaxially.—C. Very similar anatomical structure except first-order adaxial bundle sheath extension uniseriate and three cells long (arrowed).—D, E. Abaxial epidermal structure.—D. Interstomatal cells, stomata, and microhairs (arrowed) common but no other epidermal appendages present.—E. No appendages except for microhairs; two stomatal files in each intercostal zone each separated by a short interstomatal cell; costal files of three cell files, the central with alternating dumbbell-like silica bodies and cork cells (A, B, D, based on *Zuloaga et al. 4427*; C, E, based on *Zuloaga et al. 4406*; A ×100; B–E ×250).

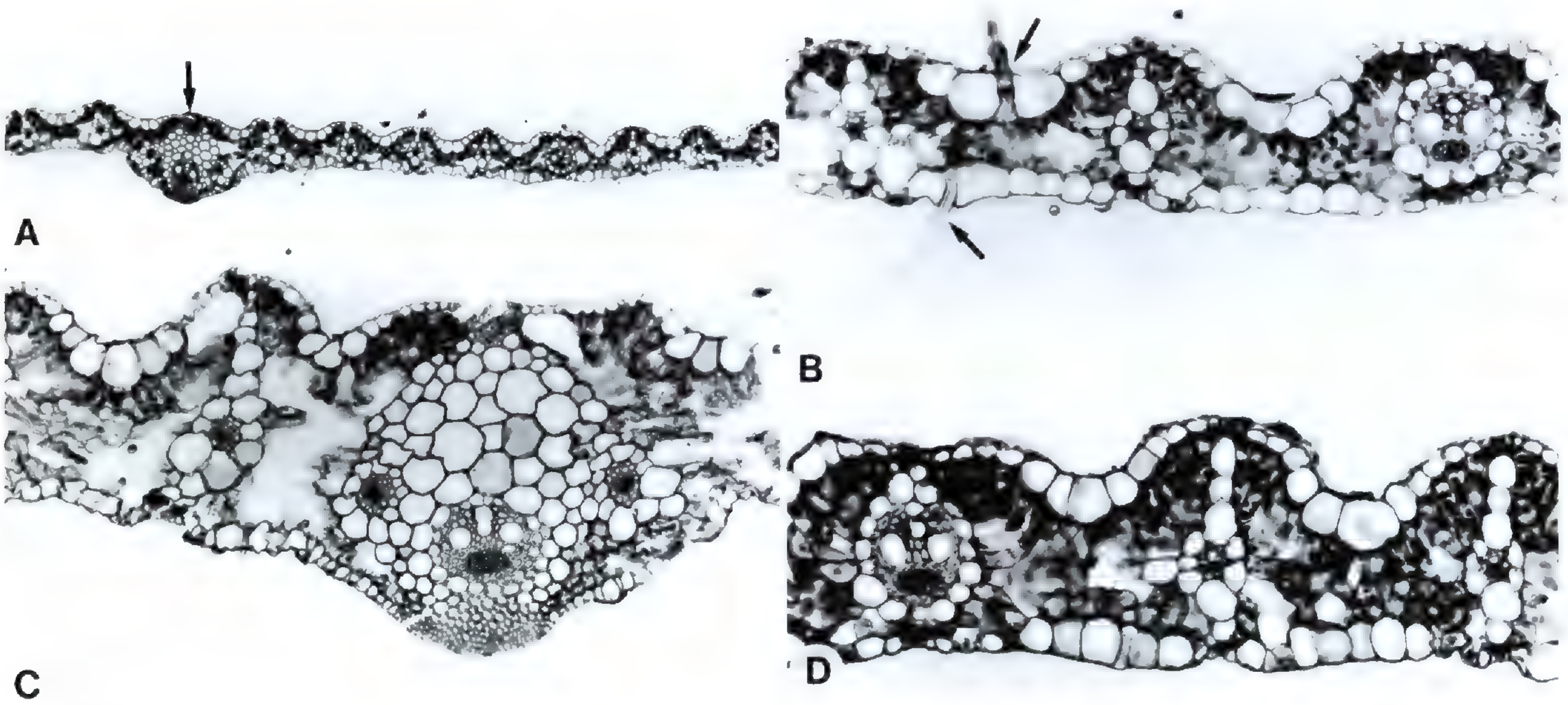


FIGURE 8. Leaf blade anatomy of *Panicum hebotes* as seen in transverse section.—A. Expanded leaf blade with keel (arrowed) incorporating three vascular bundles and adaxial parenchyma.—B. Detail of very short bundle sheath extensions, adaxial ribs, and furrows, and diffuse mesophyll tissue with large intercellular air spaces; note adaxially located chlorenchyma cells with semiradiate arrangement; adaxial and abaxial macrohairs (arrowed) present, these without raised cushion cells but inserted between unmodified epidermal cells.—C. Greater detail of keel structure showing one first-order and two third-order vascular bundles embedded in parenchymatous ground tissue.—D. Thicker leaf with longer adaxial bundle sheath extension; these cells clearly evident in the chlorenchyma cells; abaxial epidermal cells large and inflated (A, B, based on *Zuloaga et al. 2373*; C, based on *Zuloaga et al. 4534*; D, based on *Zuloaga et al. 2390*; A ×100; C ×250; B, D ×400).

sclerenchyma strands on both adaxial and abaxial surfaces. Ibs entire, of small cells with uniformly thickened walls.

*Sclerenchyma:* small, inconspicuous sclerenchyma strands associated with all vbs, both adaxially and abaxially; these strands linked to bundle sheath extensions; fibers lignified; small, rounded sclerenchyma caps located in leaf margins (Figs. 2A, 7A, 15A, 18D).

*Mesophyll:* chlorenchyma semiradiate with adaxial cells tending to a palisade-type of arrangement; abaxially located chlorenchyma cells irregular in shape, diffusely arranged with large intercellular air spaces, resembling spongy mesophyll; walls not invaginated; mesophyll varies from dense to very diffuse, irregular tissue; always more than 5 chlorenchyma cells between consecutive vbs. No colorless tissue apart from the bundle sheath extensions.

*Adaxial epidermal cells:* bulliform cells present in adaxial furrows between all vbs; usually in restricted groups with larger, fan-shaped central cells; size of bulliform cells very variable. Epidermal cells small, regular in size; no papillae or prickles, but macrohairs may be present.

*Abaxial epidermis cells:* very narrow costal zones; wide intercostal zones, often with larger, inflated, bulliformlike cells in the central files (e.g., *P. hebotes*, Fig. 8B, D); cuticle often very thin; no papillae or prickles, but macrohairs either common or absent, either with raised cushion-bases or inserted between unmodified epidermal cells as seen in section.

### Abaxial Epidermis as Seen in Surface View

*Intercostal long cells:* variable, short-rectangular (Figs. 13F, 16E) to hexagonal, resembling bulliform cells (Fig. 10C, D); side walls parallel or angled outward, end walls vertical, and anticlinal walls either unthickened or slightly thickened; rectangular cells with moderately undulating anticlinal walls but hexagonal cells usually with straight walls; intercostal cell shape variable across intercostal zones, with lateral cells being elongate and rectangular and central files being hexagonal and bulliformlike; no short cells between successive long cells except in *P. aciculare* (Fig. 1C). *Stomata:* absent in *P. aciculare* (Fig. 1C) but otherwise always present; low-triangular to low dome-shaped; two rows of stomata in each intercostal zone, these restricted to the edges adjacent to the costal zones; a single short interstomatal cell present between successive stomata in a file.

*Intercostal short cells:* absent except in *P. aciculare* (Fig. 1C), where they are tall and narrow. *Papillae:* absent. *Prickles:* absent throughout sam-

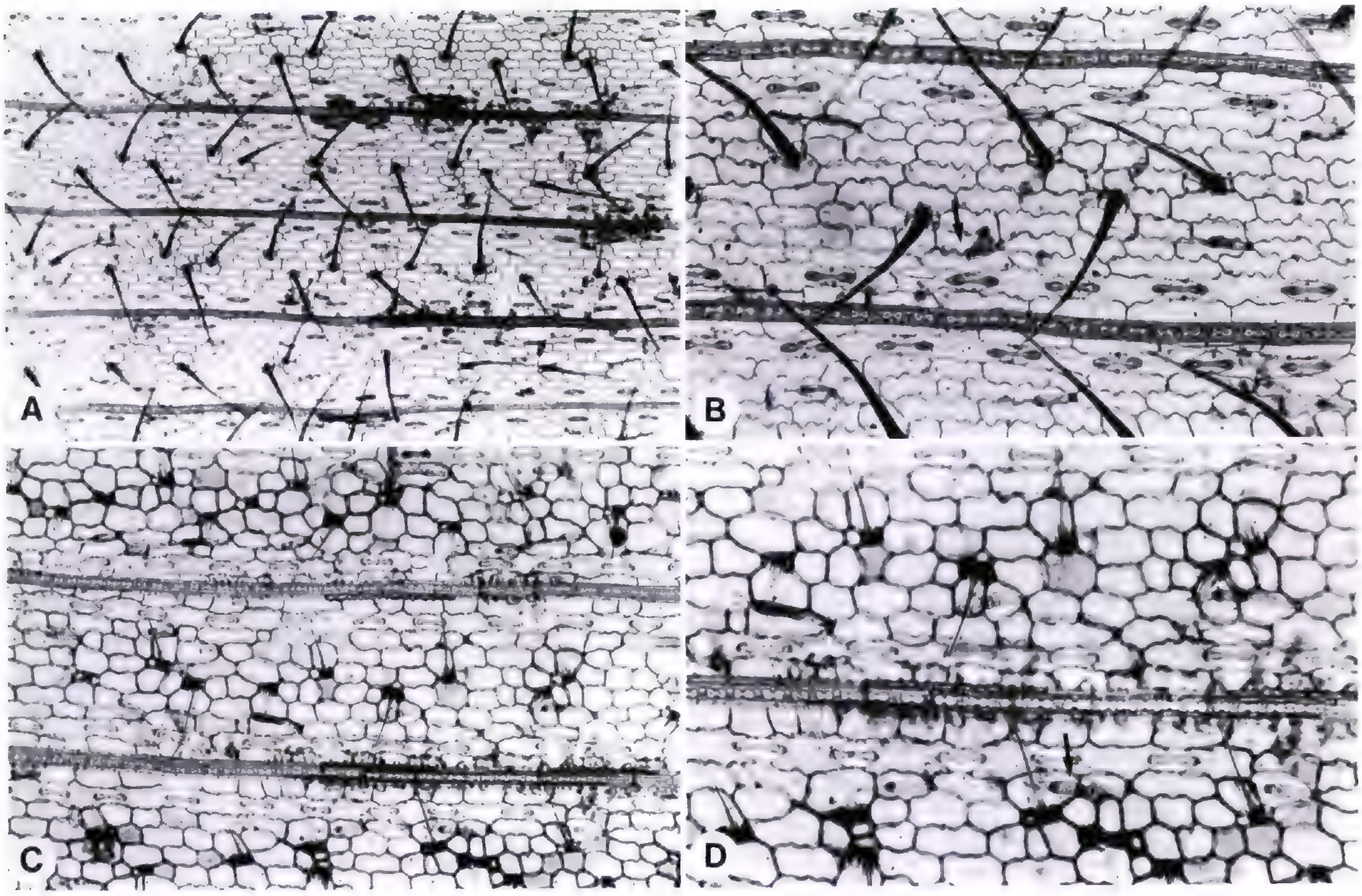


FIGURE 9. Abaxial leaf blade epidermis of *Panicum hebotes*.—A. Epidermal pattern showing marked zonation with very narrow costal zones and wide intercostal zones with numerous macrohairs.—B. Detail of irregular dumbbell-shaped costal silica bodies alternating with short, rectangular cork cells; intercostal long cells short with sinuous walls; macrohair bases associated with two specialized epidermal cells, one of which appears inflated; note that all the microhairs are three-celled (arrowed)—a very unusual configuration.—C. Typical epidermal cellular arrangement of this species; cells associated with the macrohair bases stain darkly.—D. Short intercostal long cells, macrohairs, and stomata; the microhairs (arrowed) all consist of three cells (A, B, based on *Zuloaga et al. 2373*; C, D, based on *Zuloaga et al. 2390*; A ×160; C ×250; B, D ×400).

ple. *Microhairs:* bicellular, fingerlike, with basal cell slightly shorter than distal cell; elongate, equal in length to the stomatal complexes to more than twice their length; distal cell deciduous with very thin walls; common in the central files of the intercostal zones; very rarely absent as in *P. sphaerocarpon* (Fig. 15E, F); *Panicum hebotes* always with unique tricellular microhairs (Fig. 9B, D). *Macrohairs:* either absent or present, variable in structure; two types can be recognized: long, thick hairs inserted into raised cushion-bases (Figs. 11C, 19A–D), and thin, needlelike hairs with only two specialized epidermal cells associated with the base (Figs. 6C, 9A–D, 10C, D); all intermediates occur between these extremes; recurved hairs may occur (Figs. 2D, 14D, E); macrohairs always restricted to intercostal zones; size and frequency very variable. *Silica bodies:* costal bodies irregular in shape, cross-shaped to equidimensional dumbbell-shaped to elongate dumbbell-shaped or even nodular (the latter type only overlying 3′vbs); confined to costal zones where they alternate regularly with similar-shaped or shorter cork cells; only 3 (rarely 5) files of cells per costal zone, with 1 file with silica bodies. No intercostal silica bodies.

## Discussion of Leaf Anatomy of Section *Dichanthelium*

Leaf blades in section *Dichanthelium* are typically flat, open, expanded, and symmetrical about the midrib. Leaf width is variable, including between 11 and 117 vascular bundles. *Panicum acicularе* differs from all other representatives of the section in having narrow, inrolled blades with only 11 bundles (Fig. 1A, B). This species also differs in several other respects, which may be linked to these narrow leaf blades.

The degree of development of adaxial ribs and furrows varies in section *Dichanthelium*, from complete absence to well-developed medium ribs and furrows. The full range of variation found in the section can occur in a single species, as is seen in *P. acuminatum* (Fig. 2B, C). Midrib structure is also variable, ranging from median vascular bundles structurally indistinguishable from the lateral

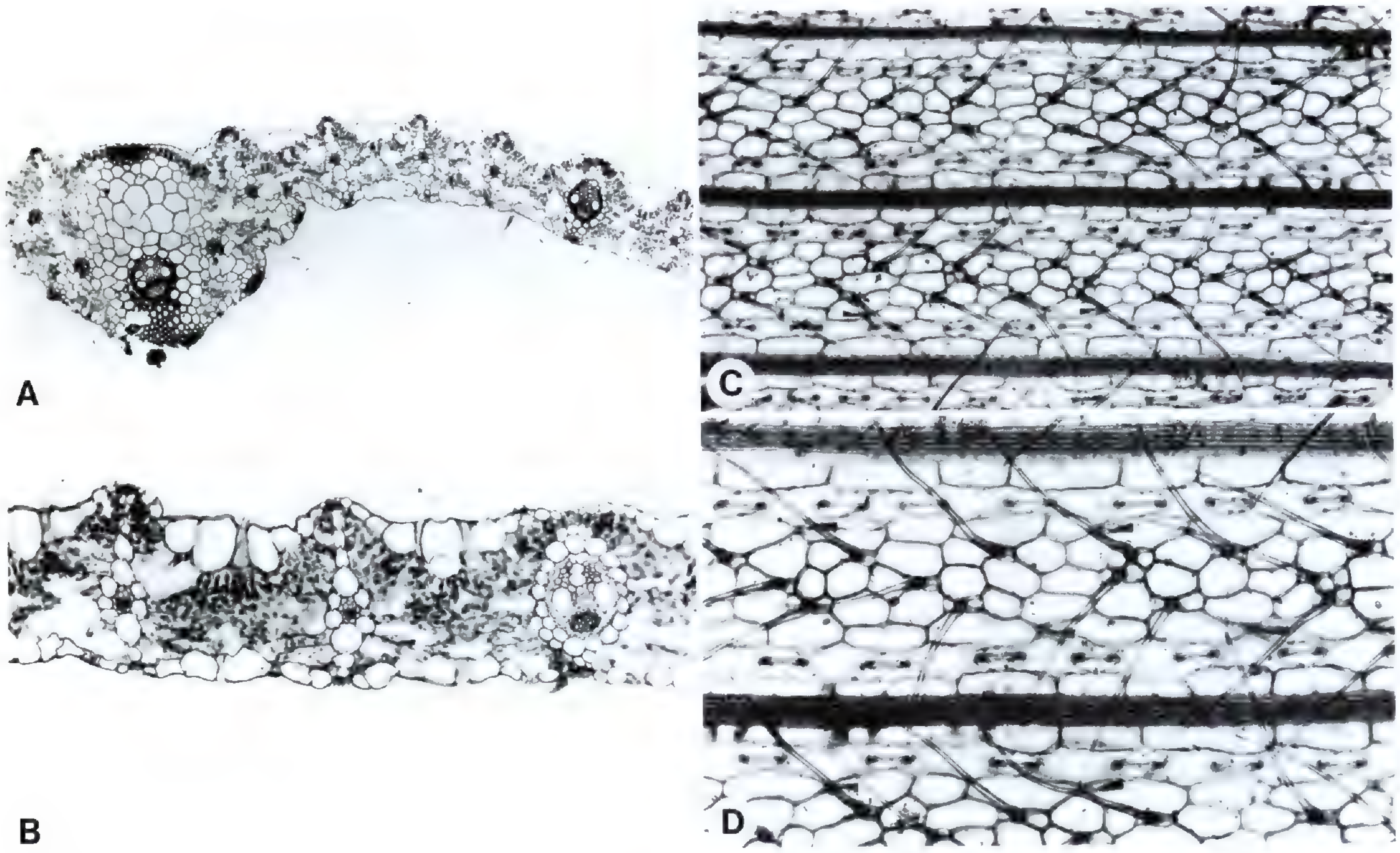


FIGURE 10. Leaf blade anatomy of *Panicum peristypum*. A, B. Anatomy as seen in transverse section.—A. Well-developed keel containing three vascular bundles and adaxial parenchyma ground tissue.—B. Detail of diffuse mesophyll and bundle sheaths and their extensions. C, D. Abaxial epidermis.—C. Epidermal pattern with very narrow costal zones and wide intercostal zones containing numerous macrohairs.—D. Detail of inflated basal cells associated with the macrohairs, bicellular microhairs, stomata, and short, irregularly shaped long cells (A–D, based on *Zuloaga et al. 2398*; A ×100; B, C ×250; D ×400).

first-order bundles to well-developed keels including up to three vascular bundles and extensive parenchyma ground tissue. Generally, each species is consistent in midrib structure, having either a median bundle, a midrib, or a keel. This is not always consistent, however; for example, all midrib types were apparent on different leaves of the same plant of *P. peristypum*.

The vascular bundle sheaths and their extensions are the most consistent and valuable anatomical character distinguishing *Dichanthelium* from the other $C_3$ taxa in *Panicum*. Colorless parenchyma

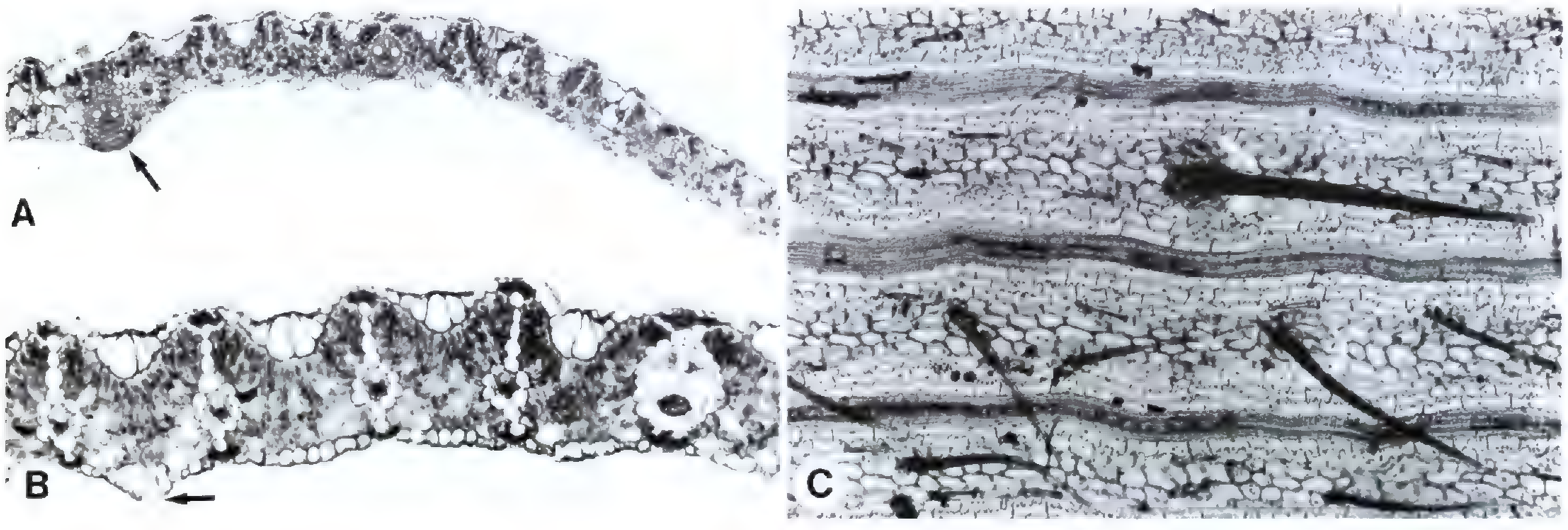


FIGURE 11. Anatomy of *Panicum pycnoclados*. A, B. Transectional anatomy.—A. Midrib (arrowed) comprising a single vascular bundle distinguishable from other first-order bundles by the large adaxial and abaxial sclerenchyma girders.—B. Rather compact mesophyll of the intermediate type with palisade and spongy tissue differentiated; third-order bundles with long uniseriate extensions; note macrohair with base inserted between raised cushion cells (arrowed).—C. Abaxial epidermis with thick macrohairs associated with cushion bases (A–C, based on *Zuloaga et al. 4404*; A ×100; B, C ×250).

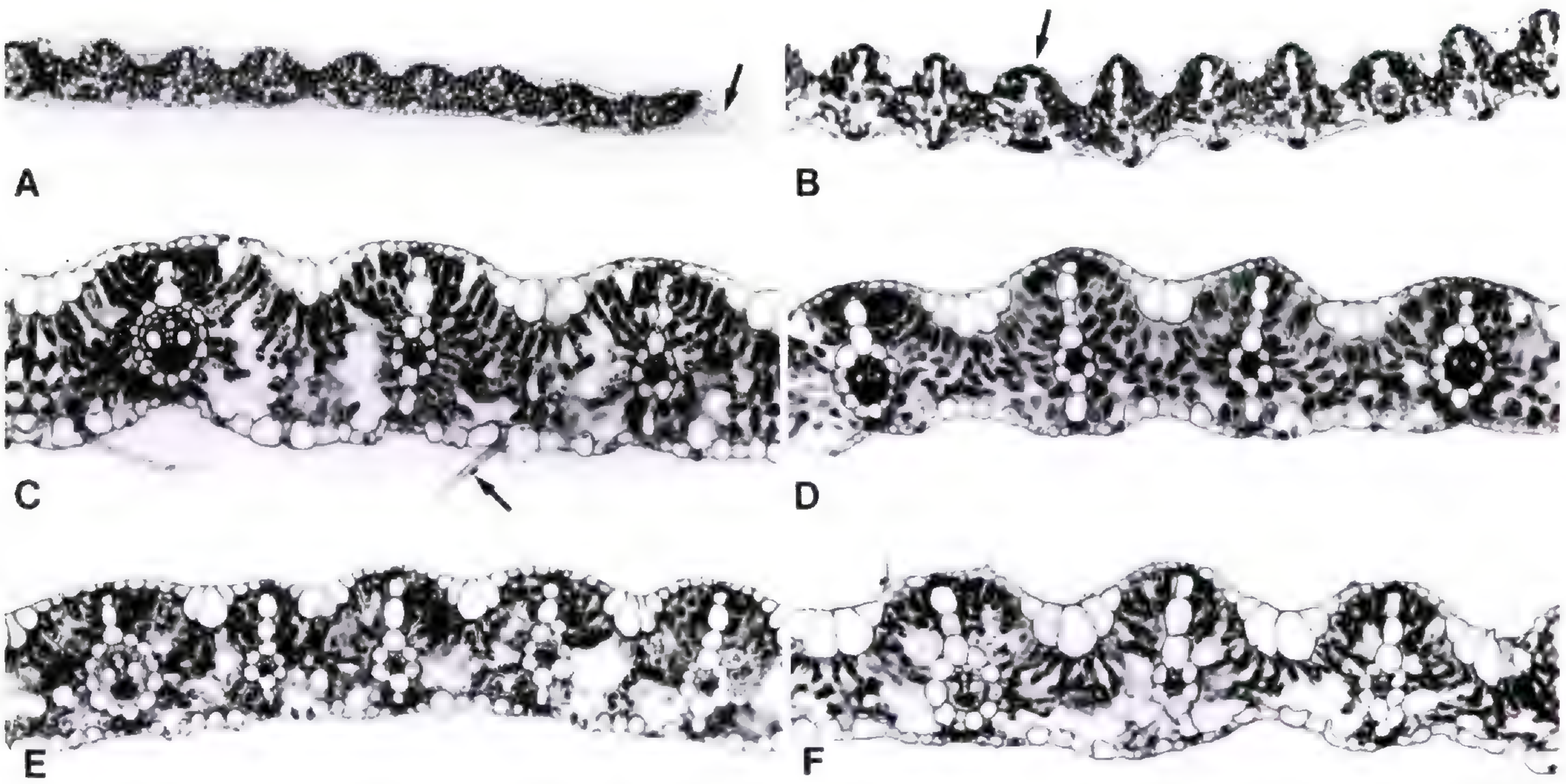


FIGURE 12. Leaf blade anatomy of *Panicum sabulorum* in transverse section.—A. Expanded blade showing margin with base of thick, cushion-based macrohair (arrowed).—B. Center of lamina with median vascular bundle (arrowed) indistinguishable from lateral first-order bundles.—C. Detail of diffuse mesophyll tending to the radiate type of arrangement; note short bundle sheath extensions and macrohairs without cushion bases (arrowed).—D. Denser mesophyll tissue with conspicuous outer bundle sheath and extension cells and small but discrete bulliform fans located in the troughs of the shallow adaxial furrows.—E. Typical anatomy of this species except that no macrohairs are present.—F. Well-developed bundle sheath extensions and very diffuse mesophyll (A, C, based on *Zuloaga 2060*; B, based on *Zuloaga 1972*; D, based on *Zuloaga 2128*; E, based on *Zuloaga 2380*; F, based on *Zuloaga 2352*; A, B ×100; C–F ×250).

sheath and extension cells are present in all taxa studied. *Panicum sphaerocarpon* (Fig. 15A–D) is an exception, as unspecialized chloroplasts appear to occur in the outer sheath and extension cells. In a few specimens of *P. viscidellum* (Fig. 20A–D), plastidlike structures are also evident in these tissues, but these appear to be found primarily in older, senescing leaves. Nevertheless, all specimens of section *Dichanthelium* examined had bundle sheath extensions, the length correlated with the thickness of the leaf blade. Section *Cordovensia* of subgenus *Dichanthelium* also has prominent adaxial bundle sheath extensions. Extensions are thus diagnostic for subgenus *Dichanthelium*, but occur sporadically in the other $C_3$ subgenus of *Panicum*, *Phanopyrum* (Raf.) Pilger, where they are found in section *Lorea* Zuloaga (*P. chnoodes* Trin. and *P. trinii* Kunth), and often in species of sections *Parvifolia* (A. Hitchc. & Chase) Pilger, *Stolonifera* (A. Hitchc. & Chase) Pilger, and *Megista* Pilger. Sections *Laxa* (A. Hitchc. & Chase) Pilger, *Parviglumia* (A. Hitchc. & Chase) Pilger, and *Phanopyrum* of subgenus *Phanopyrum* are without bundle sheath extensions, as is the intermediate $C_3/C_4$ subgenus *Steinchisma* (Raf.) Zuloaga.

The mesophyll tissue, together with the absence of specialized chloroplasts in the bundle sheath cells, indicates that section *Dichanthelium* is non-Kranz throughout. More than five chlorenchymatous mesophyll cells are always found between successive vascular bundles, implying that many chlorenchyma cells are more than two cells removed from the nearest bundle sheath cell. These parameters have been shown to predict reliably the photosynthetic pathway in grasses (Hattersley & Watson, 1975), and section *Dichanthelium* is consequently considered to be entirely $C_3$. This has been confirmed by Brown (1977) for 73 species of *Dichanthelium*.

The mesophyll tissue of section *Dichanthelium* is also of interest in that the chlorenchyma tissue does not display the irregular pattern of cellular arrangement that is normally associated with non-Kranz leaf anatomy. Instead, it is semiradiate, with the adaxially located cells palisadelike and the abaxial cells resembling spongy mesophyll tissue. This anatomy is clearly distinguishable from that of the pooid $C_3$ grasses, but most $C_3$ panicoids also have mesophyll of this type. *Panicum sphaerocarpon* (Fig. 15B) is unusual in that the adaxial chlorenchyma cells are also interspaced with intercellular air spaces, although a semiradiate arrangement is still evident.

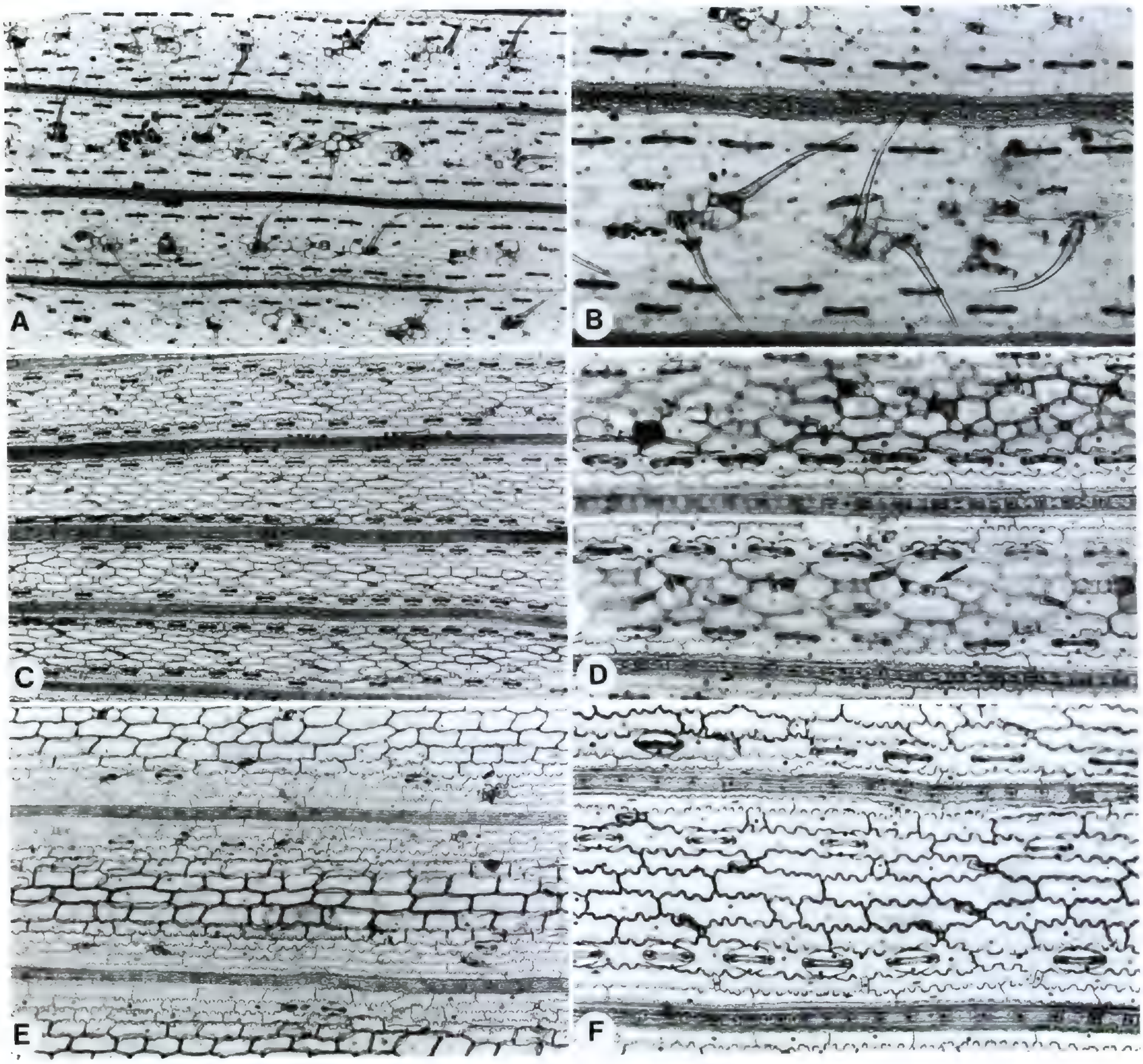


FIGURE 13. Abaxial epidermis of *Panicum sabulorum*. —A. Epidermal pattern with short macrohairs restricted to the center of the intercostal zones; note numerous stomata in two files immediately adjacent to the costal zones. —B. Detail of macrohair bases and few associated epidermal cells, irregular arrangement of dumbbell-like silica bodies in costal zones, and short bicellular microhairs. —C. Specimen without abaxial macrohairs and somewhat wider costal zones (but still consisting of three cell files). —D. Specimen without macrohairs, but note pairs of inflated epidermal cells indicative of deciduous macrohair bases (arrowed); the microhairs are clearly visible, particularly the basal cell. —E. Specimen in which the intercostal zones can be subdivided into two areas: those adjacent to the costal zones with sinuous-walled long cells, few stomata, and few microhairs, and the centrally located files which are bulliformlike; a few small macrohairs were observed in these central files. F. Intercostal zones with rectangular, sinuous-walled long cells throughout, stomata in two separate files near the costal zones and bicellular microhairs common along the central cell files (A, B, based on *Zuloaga 2060*; C, based on *Zuloaga 1972*; D, based on *Zuloaga 2128*; E, based on *Zuloaga 2352*; F, based on *Zuloaga 2380*; A, C ×160; E ×250; B, D, F ×400).

*Panicum hebotes* is unique in section *Dichanthelium* in having three-celled microhairs (Fig. 9B, D). Multicellular microhairs are rare in the Poaceae, where they have only been reported for the Guaduelleae, a primitive bambusoid tribe (Soderstrom & Ellis, 1987), lodicules of *Streptogyna crinita* (Soderstrom & Judziewicz, 1988), a few species of *Pentachistis* from the Arundinoideae (Ellis & Linder, 1991), *Paspalum* L. (Türpe, 1966) and *Panicum validum* Mez (Zuloaga et al., 1989) of the Panicoideae.

Multicellular glands are present in the abaxial intercostal zones of the epidermis of *P. adenorachis* (Morrone & Zuloaga, 1991).

## CONCLUSIONS

This study of species of *Dichanthelium* from Mexico and the West Indies to Argentina dem-

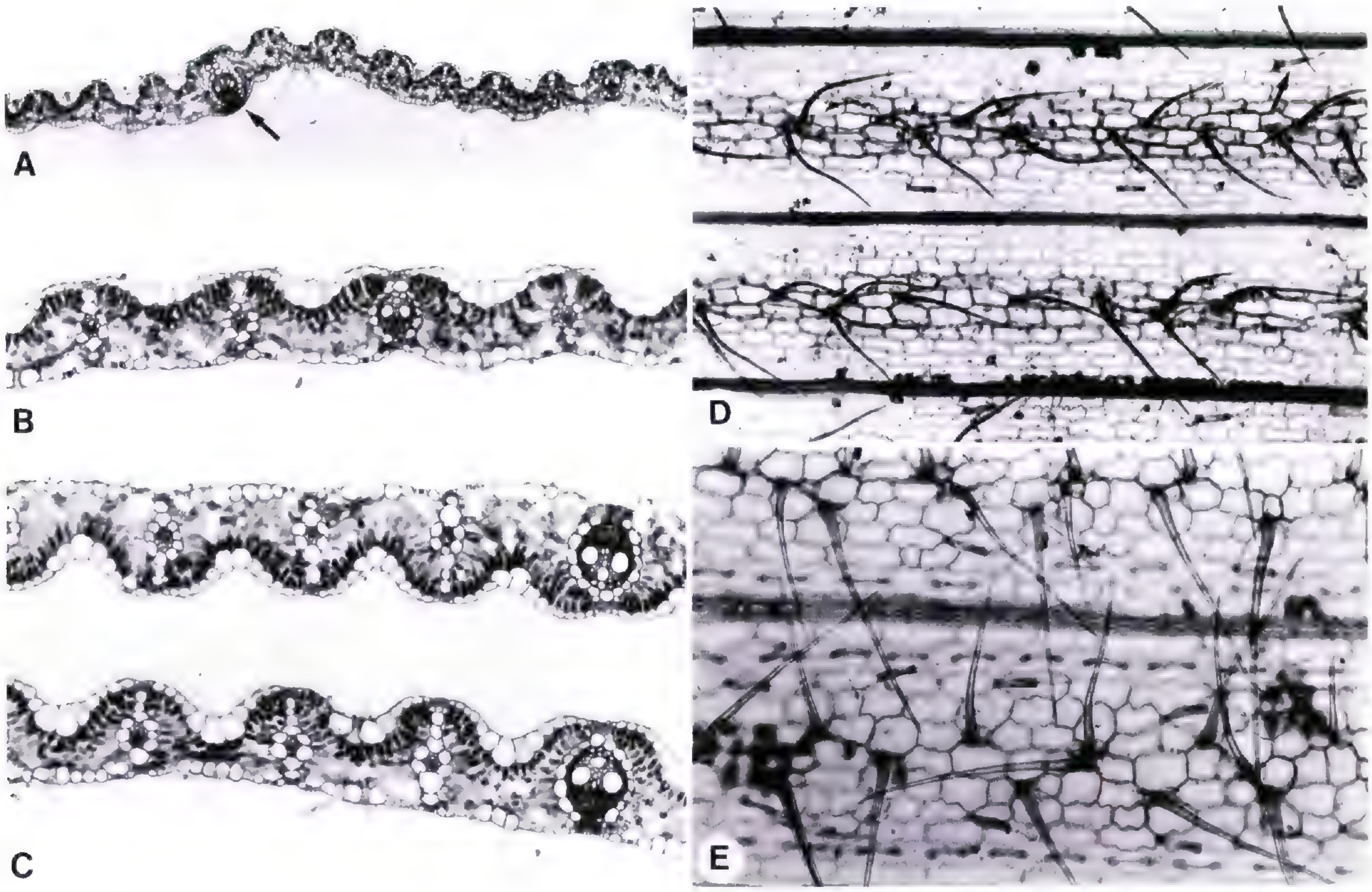


FIGURE 14. Leaf blade anatomy of *Panicum sciurotoides*. A–C. Anatomy in transverse section.—A. Central lamina showing keel with additional sclerenchyma and parenchyma development (arrowed); note macrohairs.—B. Thin blade with palisade and spongy mesophyll tissue distinguishable; bundle sheath extensions very short.—C. Thin lamina with extensive intercellular air spaces in the spongy mesophyll tissue; bundle sheath extensions visible in association with the third-order bundles. D, E. Abaxial epidermis. D. Curved macrohairs without cushion bases common along central files of intercostal zones, these files with bulliformlike cells; lateral files of intercostal zones with rectangular long cells with sinuous walls; elongate, fingerlike microhairs occur along these files (arrowed); stomata absent.—E. Detail of macrohairs and their bases, microhairs, and long cells, which are very short and irregular in shape (A, B, D, based on *Zuloaga et al. 2349*; C, E, based on *Zuloaga et al. 2354*; A ×100; B, C, D ×250; E ×400).

onstrates that there are insufficient differences to justify separation of *Dichanthelium* from *Panicum* as a distinct genus. The data presented also show a significant variation in the characters traditionally used to separate these taxa at the generic level. The rosettes and foliar and floral dimorphism are traditionally used to delimit *Dichanthelium* as a genus, but are only characteristic of species with a boreal distribution, and are absent in the rest of the species of the subgenus (Morrone & Zuloaga, 1991). This even applies to widespread species of *Dichanthelium* distributed from the United States to northern South America. Morrone & Zuloaga (1991) suggested that these characters could represent an evolutionary adaptation to harsh winters.

Gould & Clark (1978) noted that *Dichanthelium* includes mostly diploid species, with only three known polyploids. They contrasted this with *Panicum*, in which polyploid species predominate. Dubcovsky & Zuloaga (1992) confirmed the presence of additional polyploid species, including tetraploids and octoploids, in *Dichanthelium* representatives from South America. Consequently, differences in the ploidy level between *Dichanthelium* and other subgenera of *Panicum* are considered to be taxonomically insignificant.

Brown & Smith (1975) and Gould & Clark (1978) justified the separation of *Dichanthelium* from *Panicum* on the basis of the Kranz syndrome. These authors characterized *Dichanthelium* as $C_3$ or non-Kranz and *Panicum* as $C_4$ or Kranz. However, many non-Kranz species of *Panicum* are placed in subgenus *Phanopyrum* (Zuloaga, 1987), so this distinction does not seem useful in separating *Dichanthelium*. There are also no consistent differences in the ornamentation of the upper anthecium between *Dichanthelium* and other groups of *Panicum* (Zuloaga, 1987). This difference was used by Gould & Clark (1978) to distinguish *Dichanthelium* from *Panicum*.

Within *Panicum*, *Dichanthelium* can be distinguished at the subgeneric level by the following set

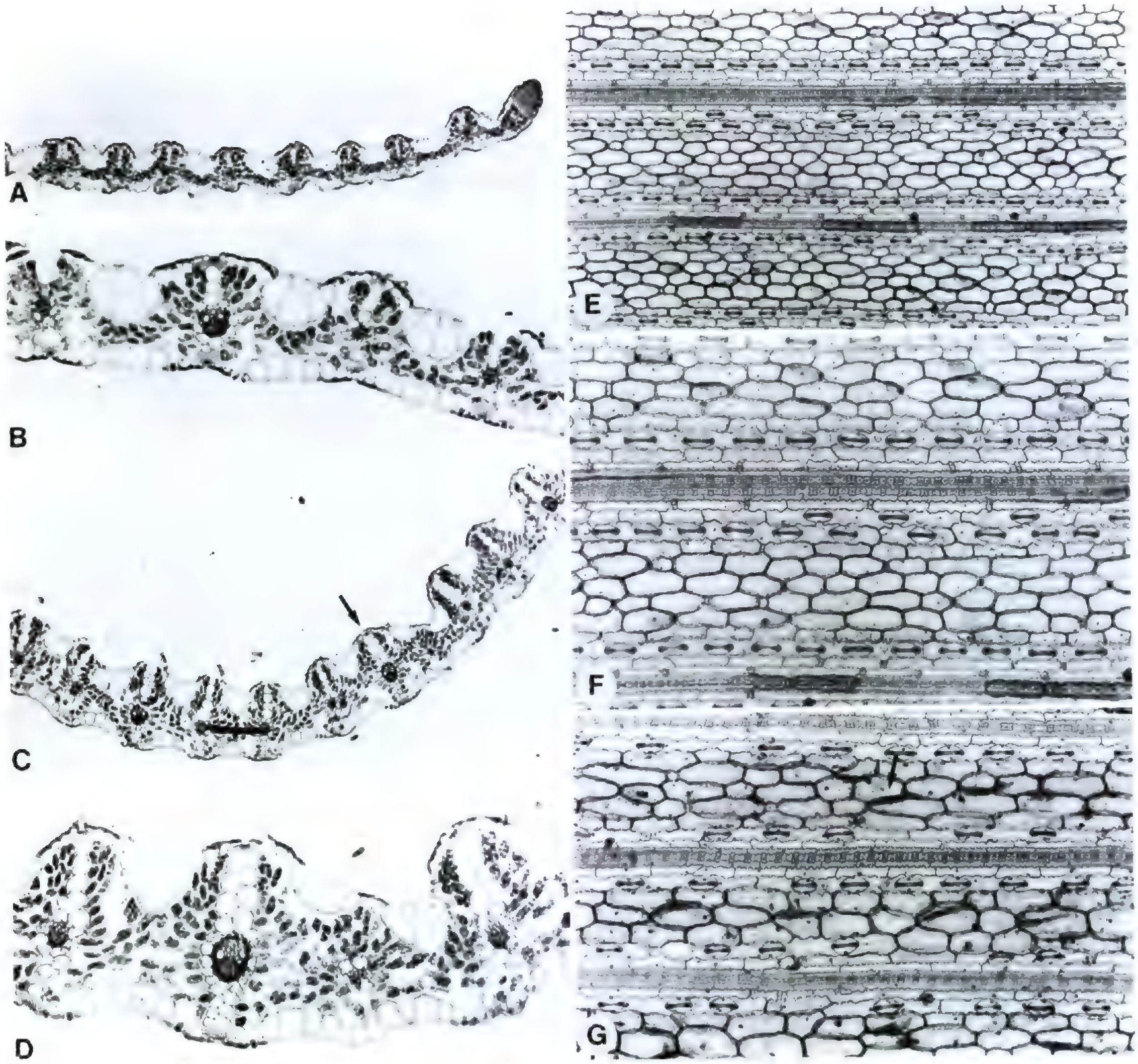


FIGURE 15. Anatomy of *Panicum sphaerocarpon*. A–D. Transectional anatomy.—A. Lateral part of expanded lamina with sclerenchyma cap in margin.—B. Detail showing large, restricted bulliform cells; note uniseriate bundle sheath extensions and thick cuticle.—C. Central part of lamina with median vascular bundle indistinguishable from other first-order bundles (arrowed); note transverse vein connecting two third-order bundles.—D. Bundle sheath extensions unusual in being biseriate (but may be uniseriate); mesophyll characteristic in that spongy and palisade tissue are not differentiated. E–G. Abaxial epidermis.—E. Epidermal pattern showing absence of macrohairs, short intercostal long cells, and two files of stomata per intercostal zone.—F. Costal zones of five cell files, two with dumbbell-shaped silica bodies; intercostal long cells with thickened periclinal cell walls, particularly the bulliformlike centrally located cells; lateral long cells more rectangular in shape with files of stomata; no microhairs evident.—G. Bicellular microhairs present in the central files of the intercostal zones (A, B, G, based on *Zuloaga 4035*; C, D, E, F, based on *Zuloaga 4249*; A, C ×100; E ×160; B, D, F, G ×250).

of characters: lax inflorescences; ellipsoid to obovoid spikelets; upper glume and lower lemma usually 7–11-nerved; upper anthecium apiculate or shortly crested, and simple papillae on the lemma and palea. Anatomically, all species are non-Kranz or $C_3$, with the outer parenchymatous sheath lacking specialized chloroplasts; a complete inner mestome sheath surrounds first-order vascular bundles; mesophyll irregularly radiating, and palisadelike toward the adaxial surface, with 5–8(–10) mesophyll cells between consecutive vascular bundles; extensions of the outer bundle sheath extending toward both epidermides and of 1–4 cells deep; dumbbell-shaped or nodular silica bodies; bicellular microhairs; and the stomatal complex dome-shaped or triangular.

Section *Cordovensia* (A. Hitchc. & Chase) L. Parodi differs from section *Dichanthelium*, as circumscribed here, in the membranous ligules, spikelets with the upper glume and lower lemma usually

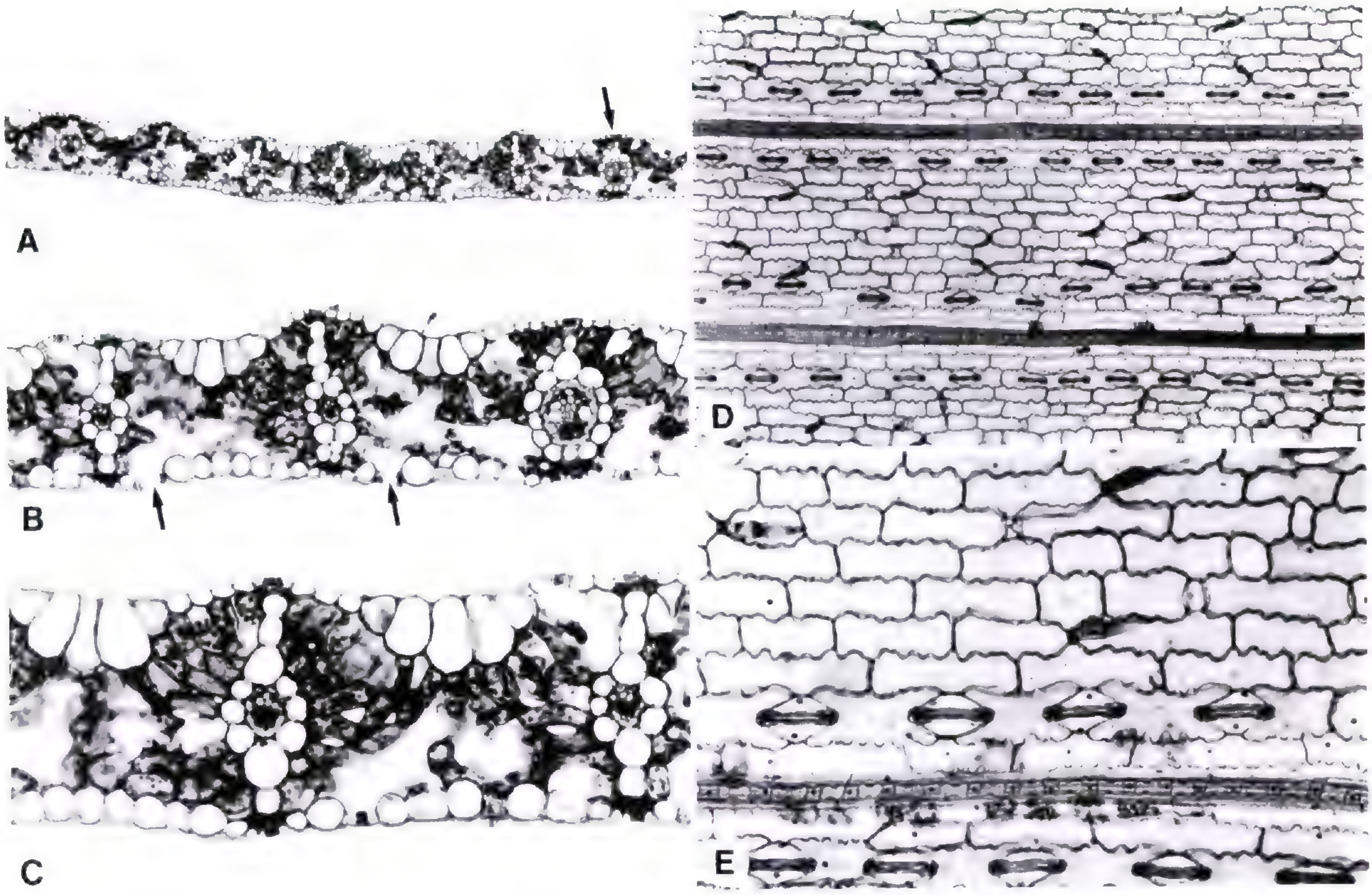


FIGURE 16. Leaf anatomy of *Panicum stigmosum*. A–C. Leaf blade in transverse section.—A. Central part of lamina showing median vascular bundle.—B. Third-order vascular bundles with uniseriate sheath extensions; note abaxial stomata (arrowed).—C. Detail showing diffuse mesophyll with large intercellular air spaces in the spongy tissue. D, E. Abaxial epidermis.—D. Epidermal zonation with wide intercostal zones and very narrow intercostal zones.—E. Detail of stomata with triangular subsidiary cells, rectangular long cells with sinuous walls, bicellular microhairs, and costal zones three cells wide with central file with dumbbell-shaped silica bodies alternating with short cork cells (A–E, based on *Zuloaga et al. 2351*; A ×100; C ×160; B ×250; D, E ×400).

5-nerved, and the lower flower and palea absent. Anatomically, species of section *Cordovensia* have midribs with rounded adaxial and abaxial projections; they have restricted groups of 5–7 large, inflated bulliform cells that lie parallel to the epidermis; the abaxial epidermis has homogeneous intercostal zones; long cells have very deeply undulating cell walls. In section *Cordovensia* the ex-

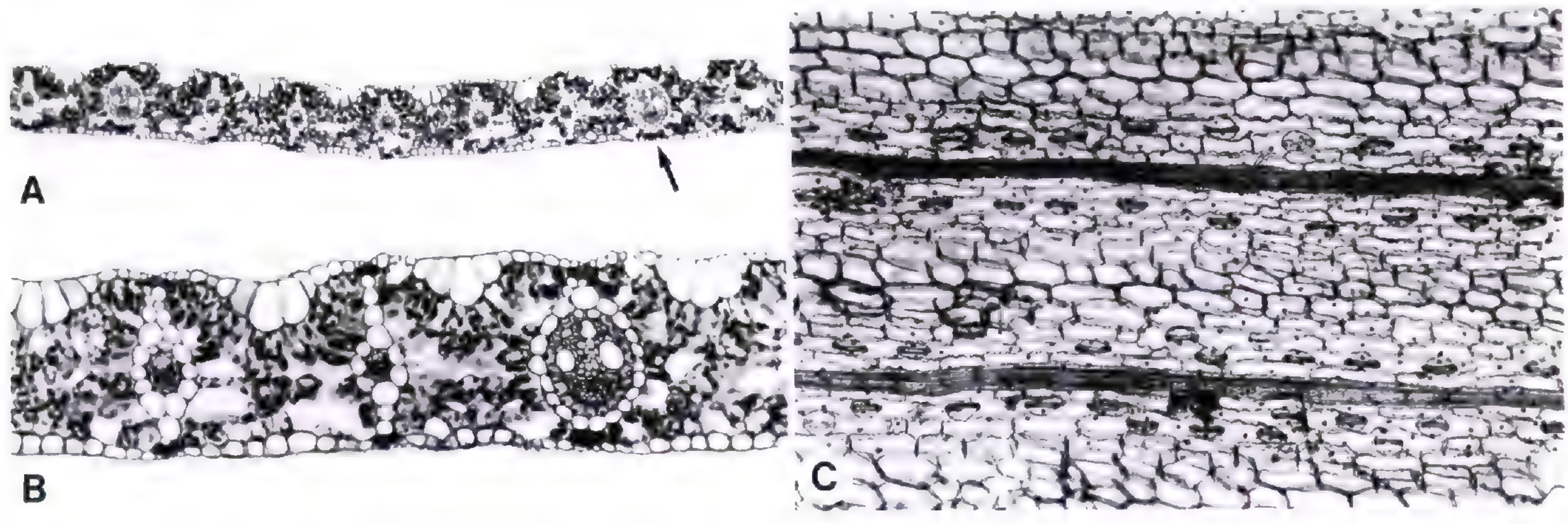


FIGURE 17. Leaf anatomy of *Panicum superatum*. A, B. Transectional anatomy.—A. Median part of blade showing median vascular bundle (arrowed) identical to other first-order vascular bundles. B. Anatomical detail of conspicuous, translucent outer bundle sheath and extension cells and diffuse mesophyll tissue.—C. Abaxial epidermis without macrohairs and with inflated, short intercostal long cells (A–C, based on *Zuloaga et al. 2374*; A ×100; B, C ×250).

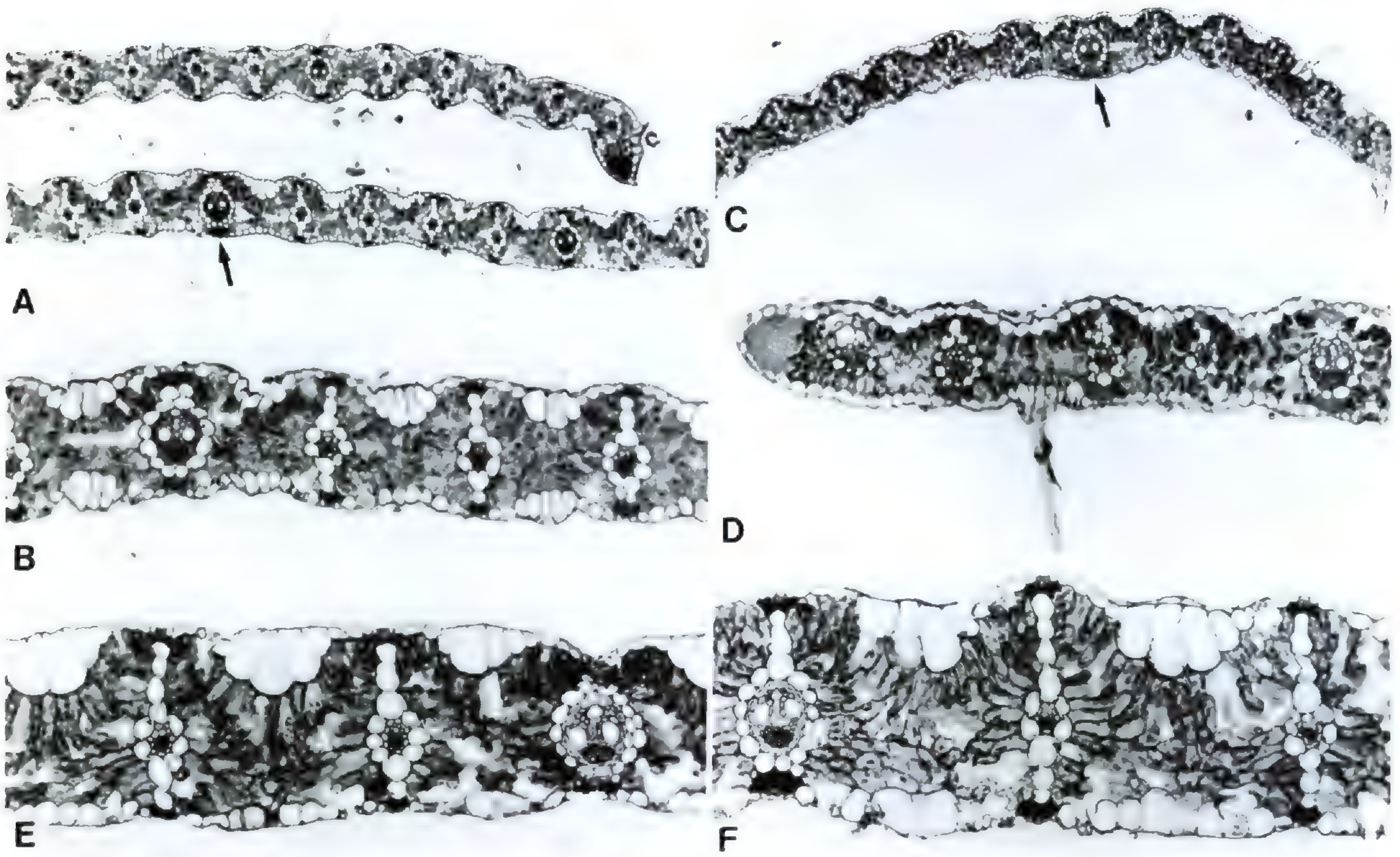


FIGURE 18. Transectional leaf blade anatomy of *Panicum viscidellum*.—A. Lateral and median part of blade showing sclerenchyma cap in margin and median vascular bundle (arrowed).—B. Detail of uniseriate bundle sheath extensions associated with third-order bundles and much shorter, biseriate adaxial extensions from the first-order bundles.—C. Midrib bundle (arrowed) with slightly larger sclerenchyma girders than are associated with the laterally located first-order vascular bundles.—D. Margin showing sclerenchyma cap and cushion-based macrohair.—E. Detail of mesophyll tissue tending to radiate type of arrangement; note intercellular air spaces and uniseriate bundle sheath extensions.—F. Chlorenchyma cell arrangement clearly evident with the adaxial cells somewhat radiately arranged whereas the abaxial tissue is irregular, resembling spongy mesophyll; note uniseriate sheath extensions and small adaxial and abaxial sclerenchyma strands associated with all vascular bundles (A, B, based on *Zuloaga et al. 4532*; C, D, based on *Zuloaga et al. 4530*; E, based on *Davidse 32336*; F, based on *Stevens 25420*; A, C ×100; B, D–F ×250).

tensions of the outer parenchymatous sheath are composed of 1(−2) cells, or are occasionally absent.

## TAXONOMIC TREATMENT

**Panicum** subgenus **Dichanthelium** A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 142. 1910. TYPE SPECIES: *Panicum dichotomum* L.

### **Panicum** section **Dichanthelium**

*Panicum* section *Dichotoma* (A. Hitchc. & Chase) Hsu, J. Fac. Sci. Univ. Tokyo, sect. 3, Bot. 9: 119. 1965. Group *Dichotoma* A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 179. 1910, nom. inval.

Perennials with or without a basal rosette of shorter, broader leaves than those of the culms. Culms erect or decumbent-erect, usually freely branching at the upper nodes; internodes hollow, with or without glands. Sheaths striate, pilose or glabrous, with or without conspicuous glands. Ligules membranous-ciliate, the membranous portion small, the cilia variable in length. Blades linear to ovate-lanceolate, flat or inrolled, densely pilose to glabrous; foliar dimorphism present or absent. Inflorescence terminal and axillary, lax, open, occasionally contracted, axis of the branches with or without glands, pilose or glabrous. Spikelets ellipsoid to obovoid, pilose or glabrous, cleistogamous flowers present or absent. Lower glume of variable length, usually ¼–⅓ the length of the spikelet, up to ¾ in several species, 1–7-nerved, acute or truncate, a short internode between the lower and upper glume present or absent. Upper glume acute to obtuse, usually not covering the apex of the upper anthecium, (5–)7–15-nerved. Lower lemma glumiform, (5–)7–15-nerved. Lower palea conspicuous, as long as its lemma to small, absent in *P. aciculare* and *P. penicillatum*; lower flower staminate or absent. Upper anthecium indurate, smooth, shiny, with simple papillae all over its surface, pilose toward the apex of the lemma or glabrous, shortly

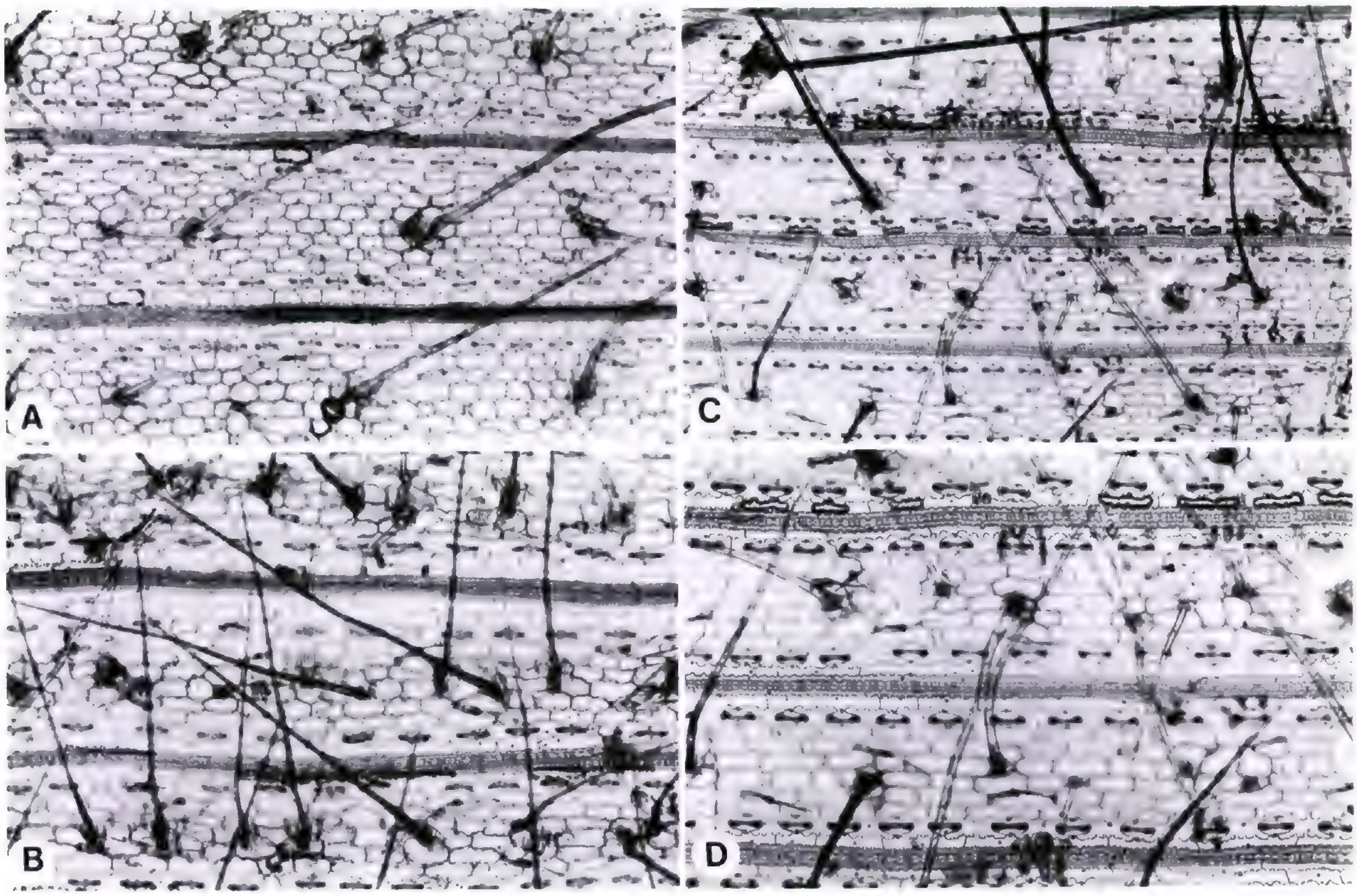


FIGURE 19. Abaxial leaf blade epidermis of *Panicum viscidellum*. — A. Prominent macrohairs common in the central files of the intercostal zones; these hairs have small cushions associated with their bases. — B. Long, slender macrohairs inserted between a few specialized epidermal cells. — C. Epidermal pattern showing narrow costal zones with files of stomata on either side; the central files of the wide intercostal zones with numerous long, slender macrohairs. — D. Detail of macrohair bases that are inserted between three or four inflated epidermal cells; numerous small elongated microhairs (A, based on *Stevens 25420*; B, based on *Zuloaga et al. 4537*; C, D, based on *Zuloaga et al. 4532*; A, C ×160; B, D ×250).

apiculate or crested; lodicules 2, conduplicate, truncate; stamens 3; styles 2, free, the stigmas 2, plumose. Caryopsis with hilum punctiform, embryo ½ or less the length of the caryopsis. Basic chromosome number: $x = 9$. Anatomy: $C_3$, non-Kranz.

A section with 37 species in Mesoamerica, the West Indies, and South America, inhabiting edges of forest in west habitats or in open places, on moist or dry sandy soils.

KEY TO THE SPECIES

1. Upper glume and lower lemma 10–15-nerved ..... 2
1. Upper glume and lower lemma (5–)7–9-nerved ..... 8
2(1). Lower palea absent; culms scandent, leaning on vegetation, to 10 m tall; internodes solid toward the base; leaf blades pseudopetiolate; lower glume as long as or a little shorter than the upper glume ..... 20. *P. penicillatum*
2. Lower palea present; culms decumbent to erect or scandent, 0.15–0.60(–2.2) m tall; internodes hollow; leaf blades not pseudopetiolate; lower glume ½–⅔ the length of the spikelet ..... 3
3(2). Inflorescences contracted; spikelets obovoid ..... 33. *P. superatum*
3. Inflorescences lax, open; spikelets narrowly ellipsoid to ellipsoid ..... 4
4(3). Spikelets 1.5–1.9 mm long ..... 27. *P. sciurotoides*
4. Spikelets 3–6.8 mm long ..... 5
5(4). Culms erect, 15–30(–60) cm tall; spikelets hirsute with papillose-pilose hairs; Mexico ..... 19. *P. pedicellatum*
5. Culms leaning on vegetation, to 2.2 m tall; spikelets glabrous; Brazil ..... 6
6(5). Spikelets 3–3.3 mm long; lower palea 2.1–2.4 mm long; lower glume 3-nerved; leaf blades with scabrous margins, ciliate toward the base; the sheaths and nodes hirsute; Venezuela and northwestern Brazil, Roraima ..... 11. *P. davidsei*
6. Spikelets 4.6–6.8 mm long; lower palea 4–5.5 mm long; lower glume 5-nerved; leaf blades with ciliate margins; the sheaths and nodes glabrous; Brazil, Rio de Janeiro and Espírito Santo ..... 7
7(6). Spikelets 4.6–5 mm long; upper anthecium 4–4.2 mm long; leaf blades 10–12 cm long ..... 17. *P. itatiaiae*
7. Spikelets 5.9–6.8 mm long; upper anthecium 5.2 mm long; leaf blades 14–21 cm long ..... 7. *P. caparaoense*

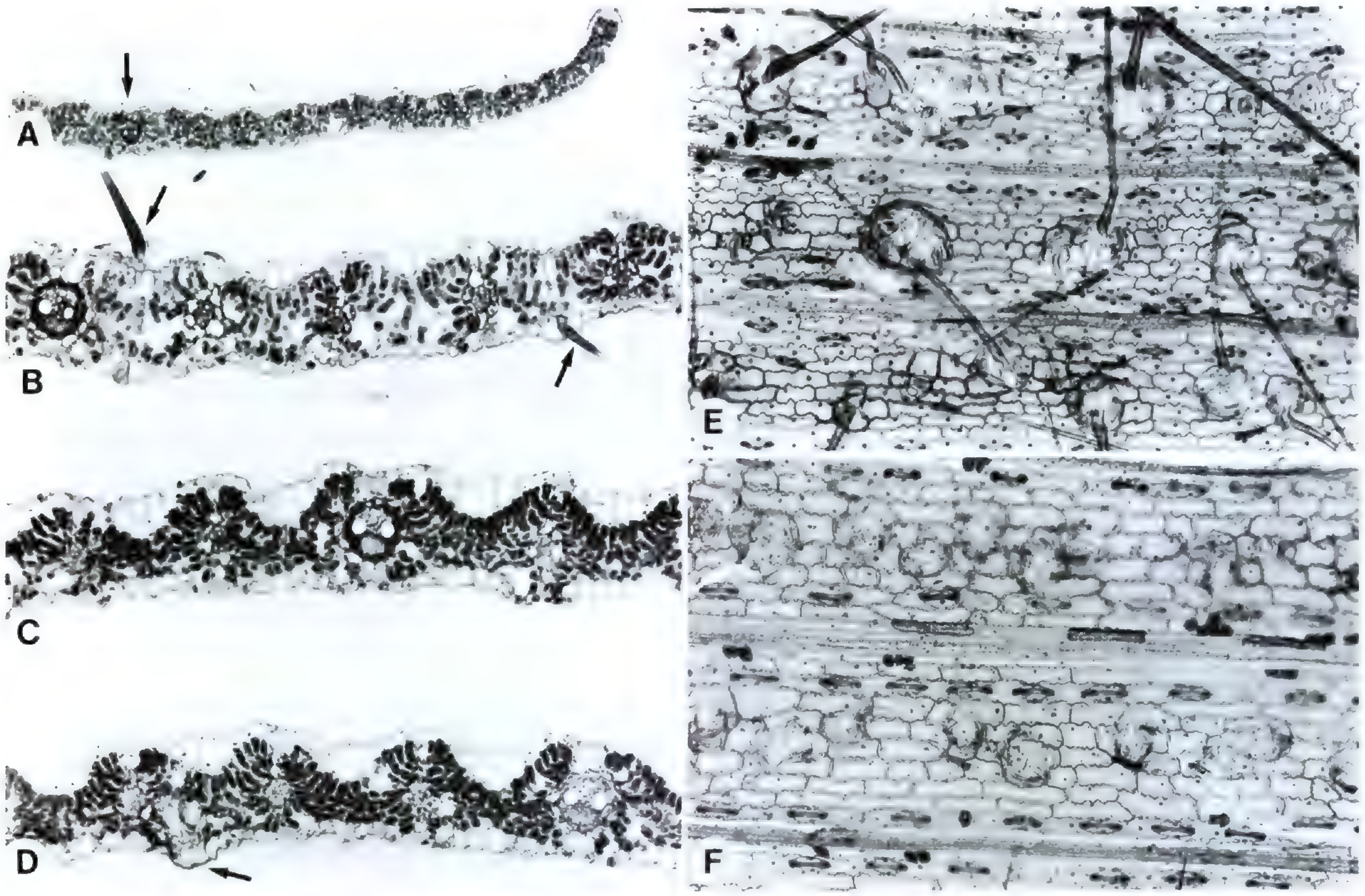


FIGURE 20. *Panicum viscidellum* specimens with silicified cushion bases of the macrohairs. A–D. Transectional leaf anatomy.—A. Leaf section showing margin and median vascular bundle (arrowed).—B. Detail of macrohairs with cushion bases (arrowed): these cushion cells do not appear to be silicified; note the outer bundle sheath cells, which contain chloroplastlike bodies.—C. Section with chloroplasts in bundle sheath and extension cells; mesophyll relatively compact.—D. Section through silicified cushion-base cells (arrowed). E, F. Abaxial epidermis.—E. Prominent macrohairs inserted into cushion bases, the cells of which are refractive, indicating silicification.—F. Specimen with small, indistinct macrohairs, but with conspicuous cushion bases that contain crystalline material resembling opaline silica (A, B, E, based on *Zuloaga & Londoño 4203*; C, D, F, based on *Zuloaga 4184*; A ×100; B–F ×250).

8(1). Spikelets usually geminate, at least in portions of the inflorescence; lower glume dimorphic; upper anthecium black at maturity; blades asymmetrical at the base ..... 15. *P. hebotes*

8. Spikelets not geminate; lower glume isomorphic; upper anthecium whitish to pale, not black at maturity; blades usually symmetrical at the base ..... 9

9(8). Lower palea conspicuous, as long as or nearly as long as the lower lemma; lower flower present or absent ..... 10

9. Lower palea small or absent, shorter than the lower lemma; lower flower absent ..... 14

10(9). Lower glume not embracing the upper glume; stipe inconspicuous between the lower and upper glume; spikelets narrowly ellipsoid, 1.8–2.2 mm long ..... 34. *P. surrectum*

10. Lower glume embracing the upper glume; stipe present between the lower and upper glume; spikelets obovoid to ellipsoid, (1.9–)2–3.2 mm long ..... 11

11(10). Inflorescences contracted, spiciform or with the first-order branches slightly divergent, the spikelets congested on the branches ..... 33. *P. superatum*

11. Inflorescences lax, first-order branches divergent, and spikelets not congested on the branches ..... 12

12(11). Spikelets ellipsoid, 3–3.2 mm long, minutely puberulent; inflorescences short-exserted or included on the upper leaves, 3–5 cm long; Serra do Sol, Venezuela ..... 35. *P. telmatum*

12. Spikelets obovoid, 1.9–3(–3.2) mm long, glabrous; terminal inflorescences exserted, 3–20 cm long; eastern Brazil, Bolivia, Paraguay, Uruguay, Chile, and Argentina ..... 13

13(12). Robust plants leaning on vegetation; leaf blades 10–22 cm long, 1–2.2 cm wide; spikelets glabrous, (1.9–)2.4–3.2 mm long; inflorescence 9–21 cm long, glandular; foliar dimorphism absent ..... 30. *P. stigmosum*

13. Caespitose or decumbent perennials not leaning on vegetation; leaf blades 1–9(–15) cm long, 0.2–1.4(–2) cm wide; spikelets hirsute to glabrous, when glabrous 1.9–2.3(–2.6) mm long; inflorescences 2–10 cm long, the axis glandular or eglandular; foliar dimorphism present ..... 25. *P. sabulorum*

14(9). Plants branching only at the base, with short internodes and basal leaves numerous in a rosette ..... 15

14. Plants normally branching above the base,

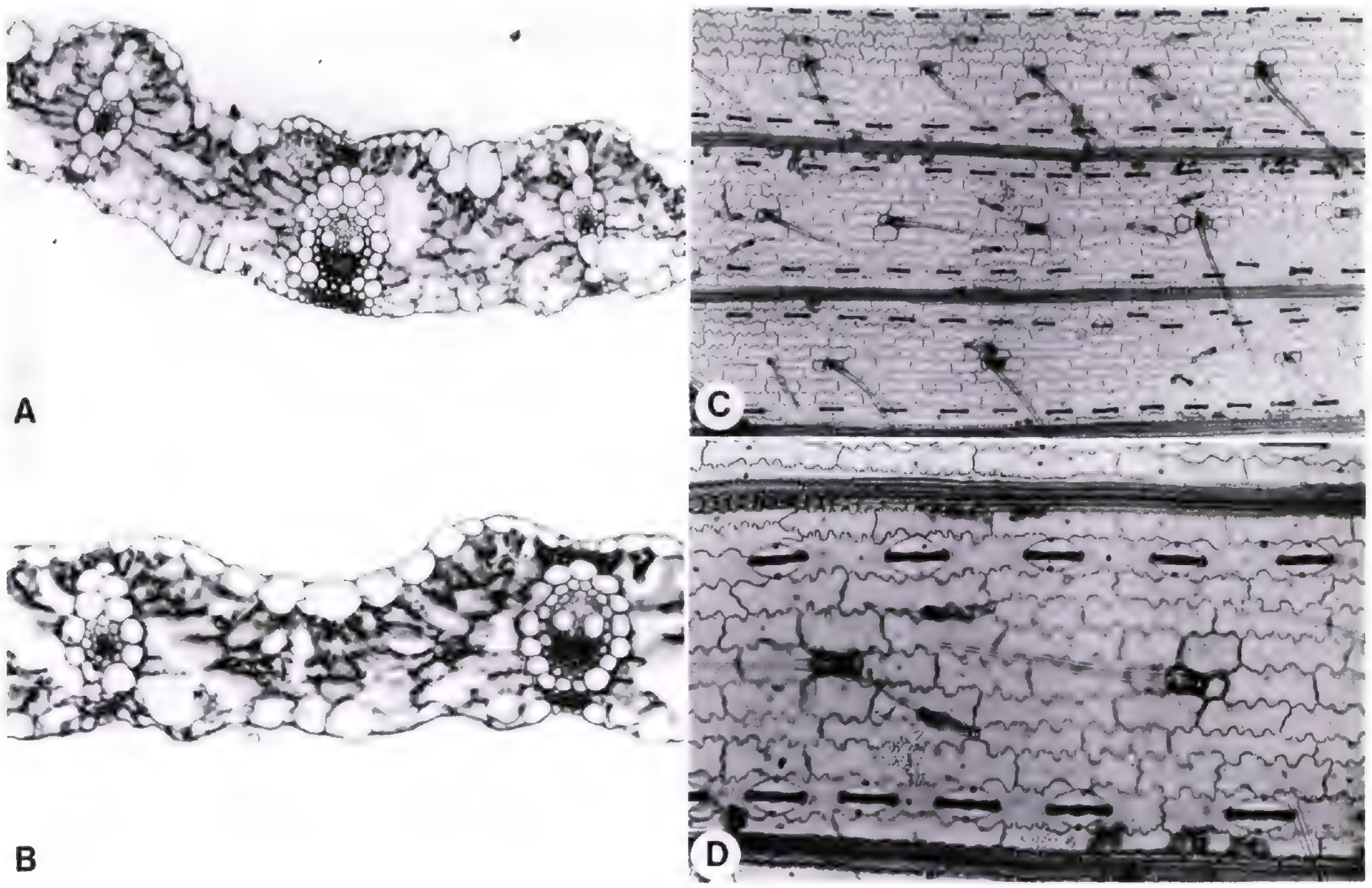


FIGURE 21. Leaf blade anatomy of *Panicum boscii*. A, B. Transectional anatomy.—A. Midrib showing slight keel development due to presence of additional parenchyma cells associated with the median vascular bundle.—B. Widely spaced vascular bundles and very diffuse chlorenchyma tissue. C, D. Abaxial epidermis.—C. Epidermal pattern showing narrow costal zones, wide intercostal zones, stomatal files, and macrohairs.—D. Detail of macrohairs and their associated basal cells, long, fingerlike microhairs, low-triangular subsidiary cells, and rectangular intercostal long cells with sinuous walls (A–D, based on *Davidse 30822*; A ×250; C ×160; B, D ×400).

with internodes elongated and basal leaves not in a rosette ..... 17

15(14). Blades linear, length : width ratio 10–30:1, with scabrous margins; caryopsis black ..... 14. *P. ensifolium*

15. Blades lanceolate to linear-lanceolate, length : width ratio 3–10:1, with long-ciliate margins; caryopsis brownish ..... 16

16(15). Spikelets 1–1.7 mm long, glabrous or puberulous; upper anthecium 1–1.4 mm long; sheaths and blades glabrous to sparsely pilose ..... 32. *P. strigosum*

16. Spikelets 2–2.7 mm long, short-hirsute; upper anthecium 1.8–2.3 mm long; sheaths and blades densely pilose with long papillose-pilose hairs ..... 18. *P. laxiflorum*

17(14). Spikelets obovoid; lower glume 1/5–1/3(–1/2) the length of the spikelet ..... 18

17. Spikelets ellipsoid; lower glume (1/4–)1/2–1/3 the length of the spikelet ..... 24

18(17). Pseudoligule present ..... 2. *P. acuminatum*

18. Pseudoligule absent ..... 19

19(18). Blades linear, length : width ratio 10–20:1; lower palea absent; inflorescences contracted, few-flowered ..... 1. *P. aciculare*

19. Blades ovate-lanceolate to lanceolate or linear-lanceolate, length : width ratio 3–10:1; lower palea present; inflorescences lax, few- to many-flowered ..... 20

20(19). Viscid glandular band present just below the nodes ..... 28. *P. scoparium*

20. Glandular band absent below the nodes ..... 21

21(20). Blades 1–7 cm long, 0.2–0.5(–1.2) mm wide; inflorescences few-flowered, 1–8 cm long, 1–3 cm wide ..... 22

21. Blades 2.5–10(–16) cm long, 0.5–1.7 cm wide; inflorescences multiflowered, (2–)5–22 cm long, 3.5–10 cm wide ..... 23

22(21). Blades narrowed at base; sheaths, nodes, and internodes glabrous to short-pilose; spikelets 0.6–1 mm wide; lower glume 1/4–1/3 the length of the spikelet ..... 12. *P. dichotomum*

22. Blades subcordate; sheaths, nodes, and internodes pilose; spikelets 1.1–1.3 mm wide; lower glume 1/4–1/2 the length of the spikelet ..... 23. *P. portoricense*

23(21). Spikelets 1–1.8 mm long; lower glume 1/3 the length of the spikelet, occasionally 1/4–1/2; axis of the panicles glabrous and glandular; blades glabrous ..... 29. *P. sphaerocarpon*

23. Spikelets (2.1–)2.3–3.2 mm long; lower glume 1/4–1/2 the length of the spikelet; axis of the panicles hispid, occasionally glabrous, with or without glands; blades with papillose-pilose hairs ..... 13. *P. divergens*

24(17). Blades clasping the culm, cordate, the length : width ratio 3–5(–7):1 ..... 25

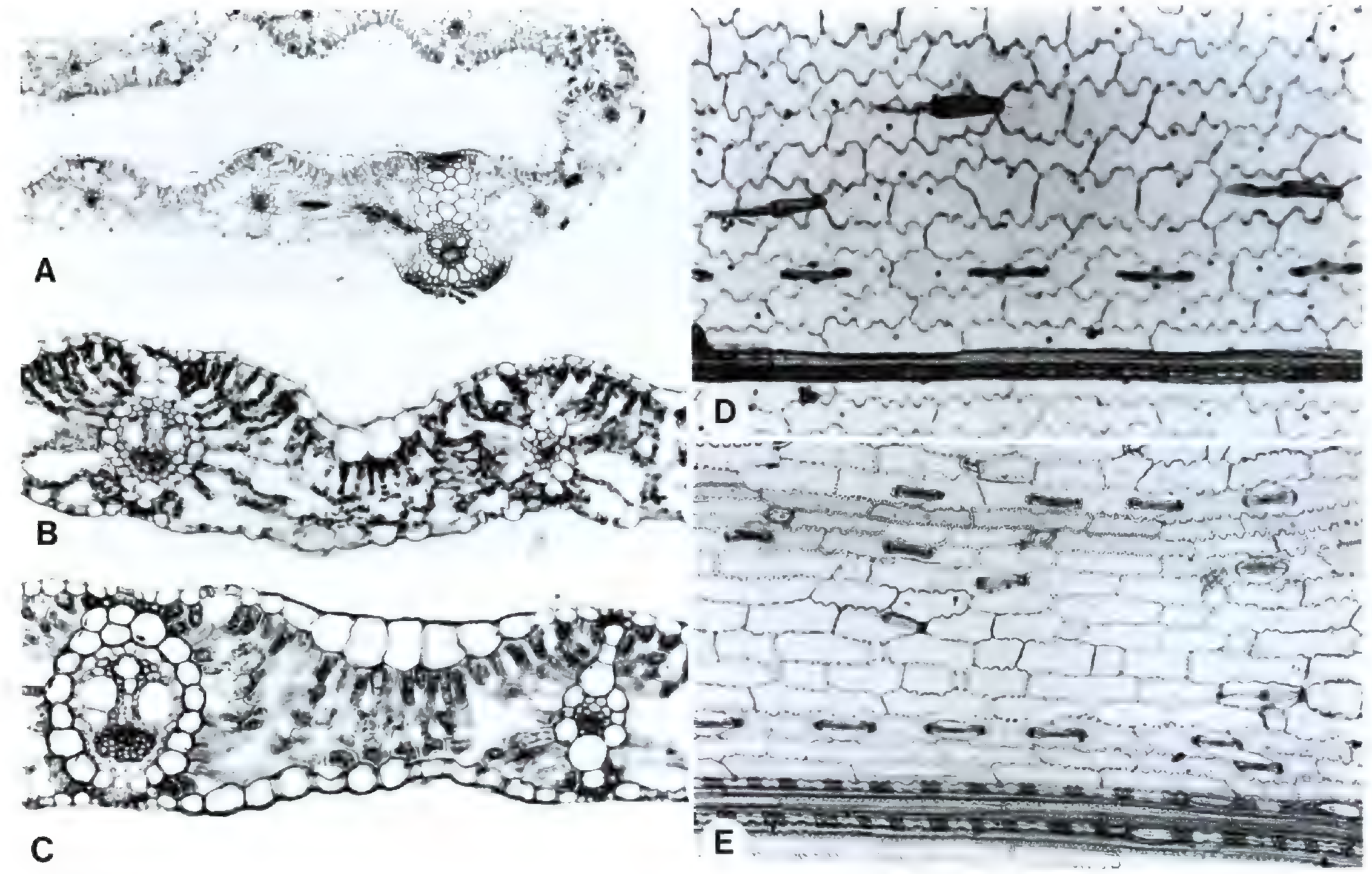


FIGURE 22. Leaf anatomy of *Panicum clandestinum*. A–C. Anatomy in cross section.—A. Central keel including a single vascular bundle.—B. Detail of diffuse mesophyll and short biseriate bundle sheath extensions.—C. Detail of spongy and palisade mesophyll and intercellular air spaces; note absence of extension on first-order bundle. D, E. Abaxial epidermis.—D. Long cells rectangular with very flexuous walls, large bicellular microhairs, and silica bodies irregularly dumbbell-shaped to nodular.—E. Thicker cuticle with less undulating long cell walls and wider costal zones; note microhairs, which are at least twice as long as the stomata (A, B, C, based on *Davidse 30816*, MO; D, E, based on *Davidse 30818*, MO; A ×100; B ×250; C, D, E ×400).

24. Blades not clasping the culm, narrowed to subcordate, the length:width ratio 10–30:1 ..... 34
25(24). Upper glume and lower lemma 5(–7)-nerved, the nerves inconspicuous; lower lemma inflated at base ..... 26. *P. sciurotis*
25. Upper glume and lower lemma 7–9(–11)-nerved, with manifest nerves; lower lemma not inflated at base ..... 26
26(25). Inflorescences few-flowered, 1–2.5(–3) cm long; blades overlapping, 1–3 cm long, 0.3–0.6 cm wide ..... 10. *P. cumbucana*
26. Inflorescences multiflowered, 2.5–12 cm long; blades not overlapping, 2–12 cm long, 0.5–2 cm wide ..... 27
27(26). Pseudoligule manifest with long whitish hairs 28
27. Pseudoligule absent ..... 29
28(27). Spikelets 2.2–2.8 mm long ..... 36. *P. umbonulatum*
28. Spikelets 1.5–2(–2.2) mm long ..... 37. *P. viscidellum*
29(27). Spikelets 1.5–2.5 mm long, without a manifest stipe between the lower and upper glume ..... 30
29. Spikelets 2.2–3.3 mm long, with a stipe between the lower and upper glume ..... 32
30(29). Spikelets short-hispid, 1.5–1.9 mm long; inflorescences 2.5–9 cm long; lower palea 0.7–1 mm long; main axis of the inflorescence densely hirsute ..... 27. *P. sciurotoides*
30. Spikelets glabrous, 1.7–2.5 mm long; inflorescences 10–15 cm long; main axis glabrous or short, sparsely pilose ..... 31
31(30). Blades amplexicaulous, ovate-lanceolate, 1.5–3 cm wide, velutinous; upper anthecium 2.2 mm long ..... 21. *P. peristypum*
31. Blades not amplexicaulous, linear-lanceolate, 0.5–1.3 cm wide, hispid or glabrous; upper anthecium 1.6–1.9 mm long ..... 4. *P. aequivaginatum*
32(29). Blades with margins cartilaginous and covered with manifest cilia ..... 31. *P. stipiflorum*
32. Blades without cartilaginous margins and without cilia on the upper portions of the margins ..... 33
33(32). Lower glume ½–¾ the length of the spikelet; inflorescences 3–6(–10) cm long; Ecuador, Peru, Venezuela, Brazil ..... 24. *P. pycnoclados*
33. Lower glume ¼–⅔ the length of the spikelet; inflorescences (5–)10–22 cm long; United States, Mexico, Honduras ..... 13. *P. divergens*
34(24). Lower glume ¼–½ the length of the spikelet ..... 35
34. Lower glume ¾–⅘ the length of the spikelet ..... 42
35(34). Pseudoligule present ..... 2. *P. acuminatum*

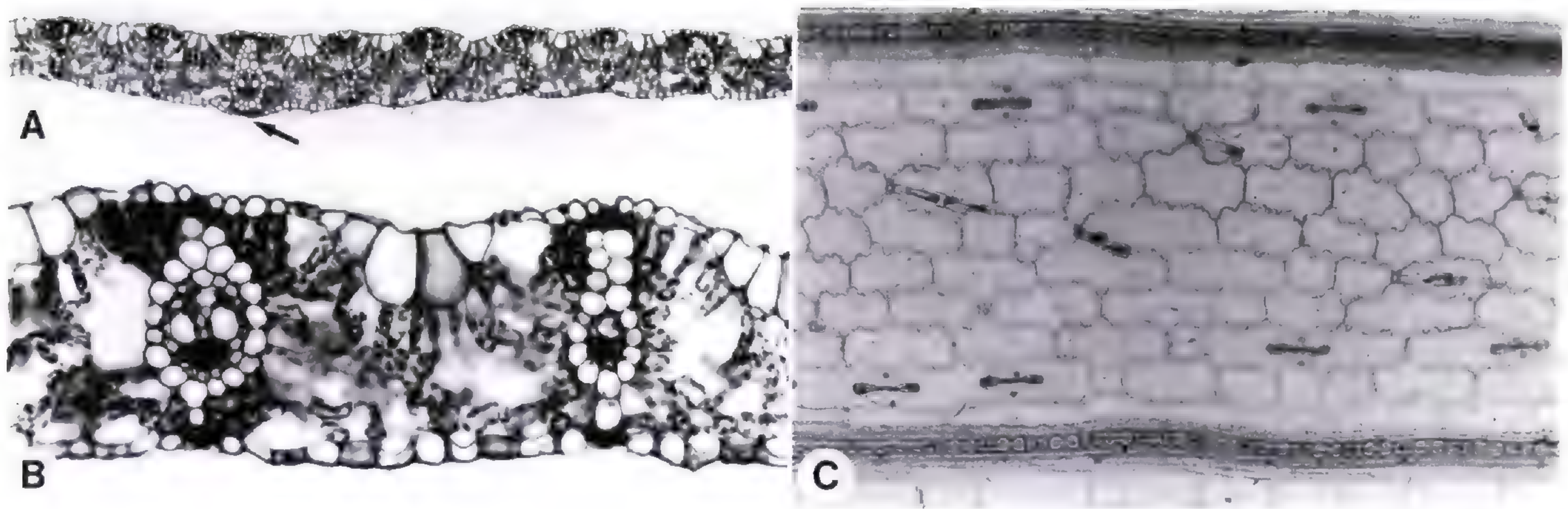


FIGURE 23. Leaf blade anatomy of *Panicum oligosanthes*. A, B. Transectional anatomy.—A. Central part of expanded lamina showing median vascular bundle (arrowed).—B. Detail of diffuse mesophyll and biseriate bundle sheath extensions.—C. Abaxial epidermis with dumbbell-shaped costal silica bodies, low triangular subsidiary cells, and bicellular microhairs; macrohairs absent (A–C, based on *Davidse 30819*, MO; A ×100; B, C ×400).

35. Pseudoligule absent ..... 36
36(35). Lower palea absent; inflorescences contracted, few-flowered; blades linear ..... 1. *P. aciculare*
36. Lower palea present; inflorescences lax, multiflowered; blades lanceolate to linear-lanceolate ..... 37
37(36). Plants densely hispid; spikelets hirsute ..... 38
37. Plants sparsely pilose or glabrous; spikelets short-hispid or glabrous ..... 39
38(37). Blades lanceolate, 3–15 cm long, 0.2–0.8(–1) cm wide, flat, the margins ciliate; spikelets 2–2.7 mm long; lower glume ⅓–½ the length of the spikelet; eastern United States to Costa Rica and the West Indies ..... 18. *P. laxiflorum*
38. Blades linear-lanceolate, 4–6 cm long, 0.2 cm wide, the margins involute, scabrous; spikelets 2–2.3 mm long; lower glume ½ or more the length of the spikelet; Brazil ..... 6. *P. cabrerae*
39(37). Blades 4–6 cm long, 0.3–0.5 cm wide; plants with manifest glands on sheaths, blades and axis of the panicles; panicles 5–7 cm long ..... 3. *P. adenorhachis*
39. Blades 3.5–12(–16) cm long, 0.2–1.3(–1.5) cm wide; plants without glands, occasionally present on the axis of the panicles; panicles 3–22 cm long ..... 40
40(39). Spikelets glabrous, 1.7–2.5 mm long; Venezuela, Guyana, and Brazil ..... 4. *P. aequivaginatum*
40. Spikelets pilose, (2.1–)2.3–4.1 mm long; United States, Mexico, and Honduras ..... 41
41(40). Spikelets papillose-pilose, 3.3–4.1 mm long ..... 19. *P. pedicellatum*
41. Spikelets sparsely pilose, (2.1–)2.3–3.2 mm long ..... 13. *P. divergens*
42(34). Spikelets with a stipe between the lower and upper glume ..... 43
42. Spikelets without a stipe between the lower and upper glume ..... 44
43(42). Spikelets glabrous, 2.2–2.7 mm long; lower glume 1(–3)-nerved; panicles lax, blades regularly spaced on the culms 9. *P. cucaense*
43. Spikelets hirsute, 2.8–3.2 mm long; lower glume 5–7-nerved; panicles contracted, blades congested on the culms ..... 8. *P. congestum*
44(42). Culms 10–25 cm tall; blades 2–5 cm long, 0.1–0.3 cm wide; panicles 2–4 cm long, spikelets glabrous, 2.4–2.6 mm long ..... 22. *P. petropolitanum*
44. Culms 50–1,000 cm tall; blades 4–32 cm long, 0.3–3.2 cm wide; panicles 4–45 cm long, spikelets pilose or glabrous, 2.6–4.2 mm long ..... 45
45(44). Lower palea absent; blades 18–32 cm long, 1.2–3.2 cm wide, pseudopetiolate; panicles 30–45 cm long ..... 20. *P. penicillatum*
45. Lower palea present; blades 4–12 cm long, 0.3–1 cm wide; panicles 4–16 cm long ..... 46
46(45). Spikelets hispid, 2.6–3.1 mm long; upper glume and lower lemma 7-nerved; blades linear lanceolate, 4–5(–12) cm long, 0.3(–1) cm wide, peduncle and main axis hirsute ..... 16. *P. heliophilum*
46. Spikelets glabrous to sparsely pilose between the nerves, 3.3 mm long; upper glume and lower lemma 9-nerved; blades linear-lanceolate, 8–12 cm long, 0.7–1 cm wide, peduncle and main axis glabrous ..... 5. *P. assurgens*

1. **Panicum aciculare** Desv. ex Poiret, Encycl. Suppl. 4: 274. 1816. *Dichanthelium aciculare* (Desv. ex Poiret) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1116. 1978. TYPE: "Habitat in India Orientali" (holotype, P; fragment, US 2808908).

Plants perennial, with or without a basal rosette of broader leaves. *Culms* erect to decumbent and geniculate at base, then erect, freely branching, 10–30(–65) cm tall, internodes hollow, terete, densely covered with short hairs, greenish to purplish, nodes compressed, brownish, pilose to glabrous. *Sheaths* shorter or longer than the inter-

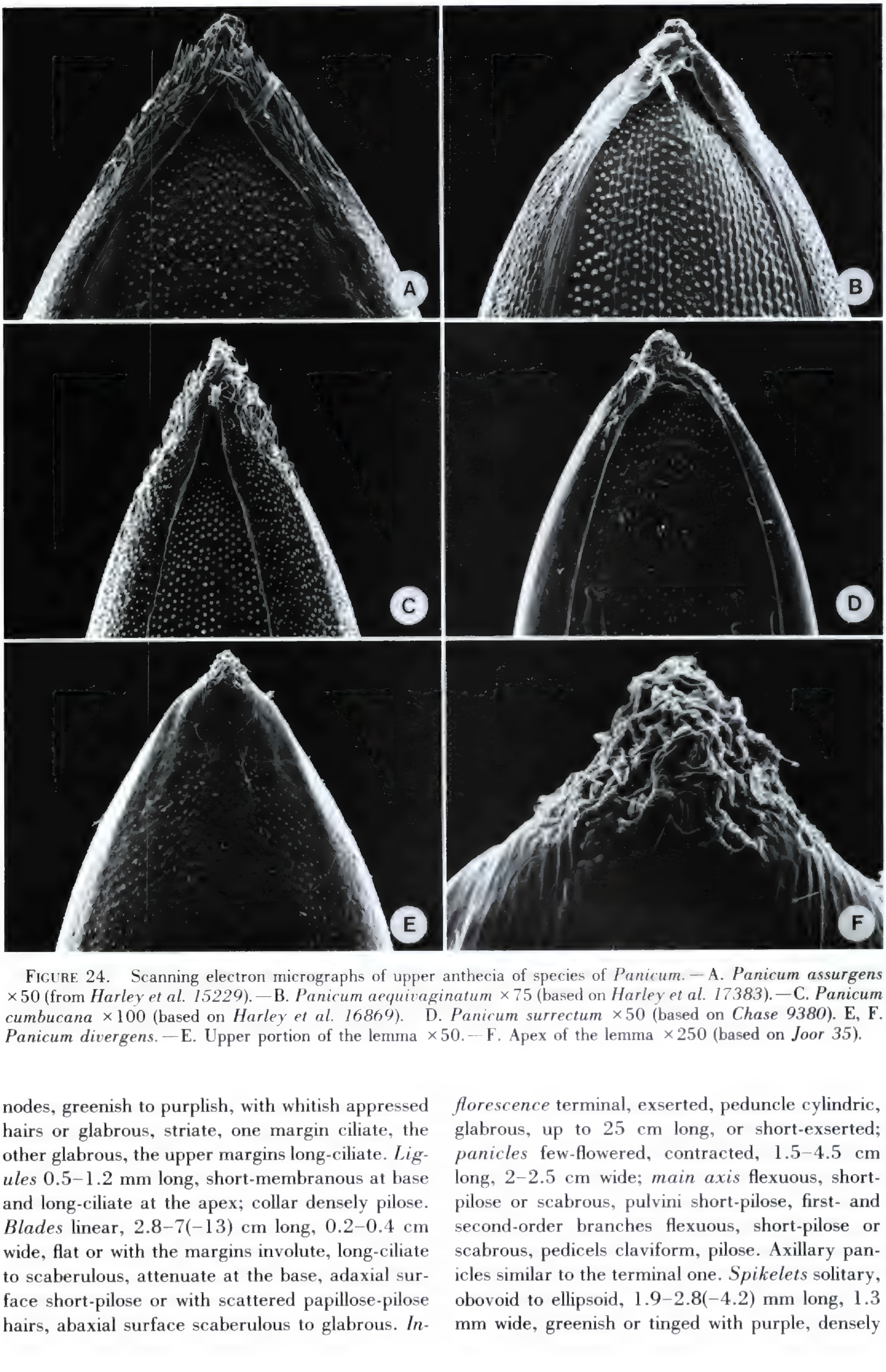


FIGURE 24. Scanning electron micrographs of upper anthecia of species of *Panicum*.—A. *Panicum assurgens* ×50 (from *Harley et al. 15229*).—B. *Panicum aequivaginatum* ×75 (based on *Harley et al. 17383*).—C. *Panicum cumbucana* ×100 (based on *Harley et al. 16869*). D. *Panicum surrectum* ×50 (based on *Chase 9380*). E, F. *Panicum divergens*.—E. Upper portion of the lemma ×50.—F. Apex of the lemma ×250 (based on *Joor 35*).

nodes, greenish to purplish, with whitish appressed hairs or glabrous, striate, one margin ciliate, the other glabrous, the upper margins long-ciliate. *Ligules* 0.5–1.2 mm long, short-membranous at base and long-ciliate at the apex; collar densely pilose. *Blades* linear, 2.8–7(–13) cm long, 0.2–0.4 cm wide, flat or with the margins involute, long-ciliate to scaberulous, attenuate at the base, adaxial surface short-pilose or with scattered papillose-pilose hairs, abaxial surface scaberulous to glabrous. *Inflorescence* terminal, exserted, peduncle cylindric, glabrous, up to 25 cm long, or short-exserted; *panicles* few-flowered, contracted, 1.5–4.5 cm long, 2–2.5 cm wide; *main axis* flexuous, short-pilose or scabrous, pulvini short-pilose, first- and second-order branches flexuous, short-pilose or scabrous, pedicels claviform, pilose. Axillary panicles similar to the terminal one. *Spikelets* solitary, obovoid to ellipsoid, 1.9–2.8(–4.2) mm long, 1.3 mm wide, greenish or tinged with purple, densely

FIGURE 25. Distribution of *Panicum aciculare* var. *aciculare*, *P. congestum*, *P. assurgens*, *P. aequivaginatum*, *P. adenorhachis*, *P. aciculare* var. *arenicoloides*, and *P. penicillatum*.

pilose or glabrescent. *Lower glume* ovate, 1.3 mm long, ⅓–½ the length of the spikelet, acute to truncate, nerveless to 3-nerved, with a small internode between the lower and upper glume. *Upper glume* ovate, obtuse, 7-nerved, hispid on the abaxial surface. *Lower lemma* 7-nerved, acute. *Lower palea* absent; lower flower absent. *Upper anthecium* obovoid, 1.8–2.1 mm long, 1.2 mm wide, pale, shiny, pilose toward the apex of the lemma, short-apiculate, lemma 7-nerved. *Caryopsis* obovoid, brownish, 1.1–1.3 mm long, 1.1 mm wide, hilum punctiform, embryo less than half the length of the caryopsis.

*Distribution and ecology:* southern United States, Mexico, Mesoamerica, the West Indies, Colombia, and Venezuela, at edge of forests or in open, wet, and sandy places between sea level and 2,400 m.

Although Poiret mentioned in the original description that the species was from "India Orientali," it was obviously collected in the West Indies.

KEY TO THE VARIETIES

1. Spikelets 1.9–2.8 mm long, without a manifest internode between the lower and upper glume ..... 1a. var. *aciculare*
1. Spikelets 2.8–3.3(–4.2) mm long, with an internode 0.3–0.6 mm long between the lower and upper glume ..... 1b. var. *arenicoloides*

**1a. Panicum aciculare** var. **aciculare**. Figures 1, 25.

*Panicum neuranthum* Griseb., Cat. Pl. Cuba: 232. 1866. TYPE: Cuba. Oriente: without locality, anno 1860, *Wright 3453* (lectotype, GOET not seen; isolectotypes, G, K, NY).

*Panicum arenicolum* Ashe, J. Elisha Mitchell Sci. Soc. 15: 56. 1898. TYPE: United States. North Carolina: in the vicinity of Chapel Hill, *Ashe s.n.* (isolectotype, NY).

FIGURE 26. Distribution of *Panicum acuminatum* var. *acuminatum*, *P. acuminatum* var. *longiligulatum*, *P. acuminatum* var. *villosum*, and *P. cabrerae*.

*Panicum chrysopsidifolium* Nash in Small, Fl. Southeast. U.S.: 100, 1327. 1903. TYPE: United States. Florida: Leon Co., Lake Jackson, 12 May 1886, *Curtiss s.n.* (holotype, NY; isotype, US 2808891).

*Selected specimens cited.* BAHAMAS. New Providence, swamp near Tea House, *Britton et al. 599* (K). BELIZE. ORANGE WALK DISTRICT: between London and Rancho along the old northern highway to Maskall, *Davidse & Brant 32927* (MO, SI). COLOMBIA. ANTIOQUIA: Río Chico Valley, 6 km NE of San Pedro, *Wood 5352* (K). BOYACA: Sáchica, 1,990 m, *Saravia 4363* (COL). CAUCA: de Balboa a Argelia, 10 km de Balboa, 2,180 m, *Zuloaga & Londoño 4201** (COL, SI). NARIÑO: Mun. La Florida, margen derecha del Río Barrancos, 2,300 m, *Díaz et al. 983* (COL). CUBA. HABANA: Batabanó, in coastal swamps, *Ekman 12581* (US). ISLA DE LA JUVENTUD: Nueva Gerona, *Ekman 11630* (G). ORIENTE: Sierra de Nipe, in pinelands at the foot of Loma Mensura, 725 m, *Ekman 6372* (G), *9066* (G, US). PINAR DEL RIO: Los Pozos, *Ekman 12794* (G, K, US). SANTA CLARA: Sabana de la Gloria, Banao Mountains, *Roca 7944* (US). DOMINICAN REPUBLIC. LA VEGA: vicinity of Piedra Blanca, *Allard 16089* (US). GUATEMALA. ZACAPA: Sierra de las Minas, *Steyermark 29707* (US). HAITI. Massif de la Selle, *Ekman 6855* (G, US); vicinity of Furcy, 1,300 m, *Leonard 4331* (US). HONDURAS. COMAYAGUA: near Siguatepeque, *Juncker et al. 5715* (US). EL PARAISO: cumbre on Yuscarán road, 1,500 m, *Standley 29366* (F, GH). FRANCISCO MORAZAN: between Cuesta de Los Muertos and Monte Obscuro, near La Montañita, *Molina 14707* (US). JAMAICA. Mason River Savanna, 2.75 mi. due NW of Kellits, 2,100–2,300 ft., *Proctor 26565* (US); Pick Lam, Upper Clarendon, *Harris 12812* (US). NICARAGUA. MATAGALPA: 5 km N of Santa María de Ostuma, between Matagalpa and Jinotega, *Williams et al. 23906* (G). PUERTO RICO. Las Marías, *Sintenis 5985* (G, US, W); Monte Mesa, vicinity of Mayagüez, *Chase 6273* (US). UNITED STATES. FLORIDA: Lake County, vicinity of Eustis, *Nash 1243* (P). NORTH CAROLINA: E of Wilmington, *Hitchcock s.n., Amer. Gr. Hb. 88* (P). VENEZUELA. ARAGUA: carretera a Choroní, 1,300 m, *Chardon 151* (US). DISTRITO FEDERAL: 5.5 km down road to Carayaca, between El Junquito and Colonia Tovar, *Davidse & Tillett 4070* (MO). FALCON: sierra de San Luis, Montaña de Paraguariba, entre el hotel Parador y Curimagua, 1,300 m, *Steyermark 85871* (VEN). LARA: selva siempreverde a lo largo de la quebrada sobre rocas calcáreas, 7 km de Barbacoas, entre Barbacoas y La Peña, *Steyermark 85862* (VEN). MIRANDA: Sebastopol, *Badillo s.n.* (US 1760675). PORTUGUESA: Dtto. Sucre, Fila del Helechal, 1,500–1,600 m, *Ramírez-Reyes 2513* (PORT).

*Panicum aciculare* is anatomically distinct from the rest of species of section *Dichanthelium* in having a narrow, inrolled leaf blade, stomata absent, and intercostal short cells occurring between

FIGURE 27. Distribution of *Panicum cucaense*, *P. cumbucana*, *P. davidsei*, *P. dichotomum*, *P. divergens*, *P. ensifolium*, *P. hebotes*, *P. heliophilum*, *P. laxiflorum*, *P. pedicellatum*, and *P. portoricense*.

the rectangular long cells. The mesophyll tissue also exhibits no pattern of cellular arrangement.

**1b. Panicum aciculare** Desv. ex Poiret var. **arenicoloides** (Ashe) Beetle, Phytologia 48: 192. 1981. *Panicum arenicoloides* Ashe, J. Elisha Mitchell Sci. Soc. 16: 89. 1900. TYPE: United States. North Carolina: New Hanover Co., near Wilmington, 7 June 1899, *Ashe s.n.* (fragment and photo, US). Figure 25.

*Panicum angustifolium* Elliott, Sketch Bot. S. Carolina 1: 129. 1816. *Panicum nitidum* Lam. var. *angustifolium* (Elliott) A. Gray, N. Amer. Gram. 2: 112. 1835. *Chasea angustifolia* (Elliott) Nieuwl., Amer. Midl. Naturalist 2: 64. 1911. *Dichanthelium angustifolium* (Elliott) Gould, Brittonia 26: 59. 1974. TYPE: United States. South Carolina: without locality, *Elliott s.n.* (holotype, CHARL not seen; fragment and photo, US).

*Panicum neuranthum* Griseb. var. *ramosum* Griseb., Cat. Pl. Cuba: 232. 1866. *Dichanthelium aciculare* (Desv. ex Poiret) Gould & C. A. Clark var. *ramosum* (Griseb.) Davidse, Novon 2: 104. 1992. *Panicum fusiforme* A. Hitchc., Contr. U.S. Natl. Herb. 12: 222. 1909. TYPE: Cuba. Without locality, anno 1863, *Wright 3454* (holotype, GOET not seen; isotypes, K, MO, NY, P, US, W, fragment and photo, US 2808979).

This variety has a similar habitat and distribution to that of variety *aciculare*.

*Selected specimens cited.* BELIZE. EL CAYO: Mountain Pine Ridge, San Agustín, *Lundell 6561* (US). ORANGE WALK: savanna ca. 5 km N of August Pine Ridge on the road to Trinidad, *Davidse & Brant 32806* (MO). TOLEDO: Swasey Branch, Monkey River, *Gentle 3903* (MO). CUBA. ISLA DE LA JUVENTUD: San Pedro, *Britton & Wilson 14305* (US). ORIENTE: Sierra Maestra, Pinar de Bayamita, *Ekman 10329* (US). PINAR DEL RIO: 17 km S of Pinar del Río, *Hitchcock 23257* (US). SANTA CLARA: sabanas W of Manacas, *León & Cazañas 5840* (US). GUATEMALA.

FIGURE 28. Distribution of *P. itatiaiae*, *P. peristypum*, *P. petropolitanum*, *P. pycnoclados*, *P. sciurotis*, *P. sciurotoides*, and *P. scoparium*.

CHIQUIMULA: on moist pine forest bank between Guatemala–Honduras border and Atulapa, 900 m, *Molina & Molina 25283* (MO, US). HONDURAS. COMAYAGUA: Coconita pass above Siguatepeque, *Williams & Williams 18842* (US). COPAN: Hacienda Espíritu Santo to Quebrada Mojanales, *Blake 7458* (US). FRANCISCO MORAZAN: faldas de la Mt. Uyuca, entre Las Flores y Quebrada El Granadillo, *Williams & Molina 14813* (US). OCOTEPEQUE: rocky hillsides of Machuca, 900 m, *Molina & Molina 27868* (MO, US). JAMAICA. Halliss Savanna, Upper Clarendon, *Harris 12234* (US); Bull Head Mountain and vicinity, *Hitchcock 9552* (US). MEXICO. CHIAPAS: Mun. Palenque, 8–12 km N of Palenque on road to Catazaja, *Breedlove & Davidse 55333* (MO). NICARAGUA. San Rafael del Norte, 1,200–1,350 m, *Miller & Griscom 132* (US). VENEZUELA. MIRANDA: Sebastopol, *Badillo*, Aug. 1938 (US).

**2. Panicum acuminatum** Sw., Prodr. 23. 1788. *Dichanthelium acuminatum* (Sw.) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1123. 1978. TYPE: Jamaica. Without locality, *Swartz s.n.* (holotype, S not seen; fragment and photo, US 2808906; isotype, M).

Plants perennial, 10–35(–60) cm tall; *culms* decumbent and geniculate, then erect, branching at the middle and upper nodes; internodes 2–5 cm long, hollow, striate, densely hirsute or glabrous, nodes densely pilose with whitish retrorse hairs or glabrous. *Sheaths* 1–5 cm long, striate, greenish to purplish, short-pilose, hirsute, the margins largely ciliate or glabrous. *Ligules* membranous-ciliate, 0.2–1 mm long, with a pseudoligule formed by long, whitish hairs up to 4 mm; collar puberulous to densely pilose. *Blades* linear-lanceolate to lanceolate, 2–6.5(–9) cm long, 0.2–0.8(–1) cm wide, subcordate, acute, flat, long-hispid to glabrous on the adaxial surface and pilose on the abaxial one, the margins scabrous to ciliate, the basal ones long-ciliate. *Inflorescence* terminal, long-exserted, peduncle hispid, up to 30 cm long; panicles lax,

FIGURE 29. Distribution of *Panicum sphaerocarpon* var. *floridanum*, *P. sphaerocarpon* var. *sphaerocarpon*, *P. stigmosum*, *P. stipiflorum*, and *P. strigosum*.

diffuse, multiflowered, 2–4.5(–9) cm long, 1–4(–9) cm wide; *main axis* flexuous, long hispid to nearly glabrous, glands occasionally present, first- and second-order branches flexuous, glabrous to sparsely pilose, glands occasionally present, pulvini densely pilose, pedicels terete, sparsely pilose or glabrous. Axillary panicles numerous, smaller than the terminal one, short-exserted. *Spikelets* obovoid or ellipsoid, (0.9–)1.5–2(–2.4) mm long, 0.7–1 mm wide, hispid, greenish to purplish, without an internode between the lower and upper glume, upper glume and lower lemma subequal. *Lower glume* ovate-acuminate, 0.6–0.8 mm long, ⅓–½ the length of the spikelet, obtuse to truncate, 1(–3)-nerved. *Upper glume* ovate, 1.5 mm long, 9-nerved. *Lower lemma* glumiform, 7–9-nerved. *Lower palea* lanceolate, small, 0.6–0.9 mm long, 0.3 mm wide, hyaline, glabrous, lower flower absent. *Upper anthecium* ovoid, 1.3–1.5 mm long, 0.9 mm wide, globose, pale, shiny. *Caryopsis* ellipsoid, 1 mm long, 0.7 mm wide, hilum punctiform, embryo ⅓ the length of the caryopsis.

KEY TO THE VARIETIES

1. Spikelets 0.9–1.5 mm long, blades glabrous or sparsely pilose with hairs up to 0.1 mm long ... 2b. var. *longiligulatum*
1. Spikelets 1.5–2.4 mm long, blades usually densely pilose ... 2
2. Spikelets 1.5–1.9(–2.4) mm long, the leaves not densely pilose, the hairs only 0.4–1.5 mm long ... 2a. var. *acuminatum*
2. Spikelets 1.9–2.4 mm long, leaves densely pilose with hairs 2–4 mm long ... 2c. var. *villosum*

**2a. Panicum acuminatum** var. **acuminatum**. Figures 2, 3, 4, 26.

*Panicum tennesseense* Ashe, J. Elisha Mitchell Sci. Soc. 15: 52. 1898. *Panicum lindheimeri* Nash var. *tennesseense* (Ashe) Farwell, Amer. Midl. Naturalist 11: 45. 1928. TYPE: United States. Tennessee: La Vergne Co., 7 Aug. 1897, *Biltmore Herb. 7087* (holotype, US).

*Panicum commophyllum* Nash, Bull. Torrey Bot. Club 30: 380. 1903. TYPE: Puerto Rico. Santurce, 9 Jan. 1899, *Heller & Heller 12* (holotype, NY; fragment, US 80593).

FIGURE 30. Distribution of *Panicum surrectum* and *P. viscidellum*.

*Panicum olivaceum* A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 225. 1910. TYPE: Guatemala. Alta Verapaz: Cobán, 1,400 m, Feb. 1888, *von Tuerckheim 428* (holotype, US; fragment, US 823309; isotype, US).

*Distribution and ecology:* United States, Mexico, the West Indies, Mesoamerica, and northern South America in Colombia, Ecuador, and Venezuela, growing in forests, moist banks, and open ground, from sea level to 2,800 m.

*Selected specimens cited.* BELIZE. BELIZE: Belize International Airport, *Dwyer 9110* (MO). CAYO: Mountain Pine Ridge, along Coona Cairn Road, *Davidse & Brant 33054* (MO). STANN CREEK: Mullins River pine ridge, *Gentle 8551* (US). TOLEDO: Monkey River, near Jenkins Creek, *Gentle 4122* (MO, US). COLOMBIA. ANTIOQUIA: Medellín, 2,000 m, *Archer 1077* (US). BOYACA: entre Chinavita y Tibaná, 1,700 m, *Zuloaga & Londoño 4119, 4120* (COL, MO, SI). CAUCA: de Balboa a Argelia, 10 km de Balboa, 2,180 m, *Zuloaga & Londoño 4202** (MO, SI). CUNDINAMARCA: subida a Alto del Tigre, 1,700 m, *Zuloaga 4025* (COL, MO, SI). MAGDALENA: Santa Marta, *Smith 2140* (G, K, MO, NY, P, US). NARIÑO: San José de Albán, 1,800 m, *Martínez & Martínez 59* (COL). RISARALDA: Mun. Santuario, vereda San Rafael, Los Planes, por la carretera hacia Pueblo Rico, 2,000 m, *Camargo & Londoño 7281* (COL). VALLE DEL CAUCA: Hoya del Río Cali, Pichinde, *Cuatrecasas 18559* (US). COSTA RICA. CARTAGO: La Estrella, *Standley 39320* (US). GUANACASTE: Cordillera de Guanacaste, Volcán Rincón de la Vieja, Hacienda Guachipelín, *Pohl & Davidse 11676* (US), *11677* (MO). SAN JOSE: between Aserrí and Tarbaca, 1,900 m, *Standley 34048* (US), 1,675 m, *Davidse & Pohl 972* (MO). CUBA. ISLA DE LA JUVENTUD: near Nueva Gerona, *Curtiss 307* (G, M, P, US). ORIENTE: Sierra Maestra, Pinar de Bayamita, *Ekman 10330* (G, US). PINAR DEL RIO: environs de Sumidero, *León & Schafer 3472* (P, US). SANTA CLARA: at the mines of Motembo, *Ekman 16841* (US). DOMINICAN REPUBLIC. Loma de la Sal, 1,300–1,400 m, *Liogier 13365* (NY). LA VEGA: vicinity of Jarabacoa, 500–1,200 m, *Allard 14508* (US). SAN JUAN: Sabana Nueva, Cordillera Central, N of Río Arriba, 6,200 ft., *Howard 9162* (P, US). ECUADOR. IM-

FIGURE 31. Distribution of *Panicum superatum*, *P. telmatum*, and *P. umbonulatum*.

BABURA: Collapi, 840 m, *Acosta-Solìs 12834* (F, US). PICHINCHA: without locality, *Padilla 1122* (MO). EL SALVADOR. CHALATENANGO: along Hwy. 4, 4 km SSE of La Palma, *Pohl & Davidse 11894* (MO). GUATEMALA. ALTA VERAPAZ: along Río Cachá, 1,360 m, *Standley 89929* (US). EL QUICHE: 2 km NW of Nebaj, *Metzler 21* (MO). HUEHUETENANGO: Cerro Cananá, between Nucapuxlac and Cananá, Sierra de los Cuchumatanes, 2,500–2,800 m, *Steyermark 49025* (US). IZABAL: trail from Los Amantes to Izabal, *Blake 7739, 7762, 7780* (US). PETEN: 1 km N of Poptún, *Harmon & Dwyer 2708* (MO). SOLOLA: pine woods bordering Río Bravo, in vicinity of Finca Mocá, S-facing slopes of Volcán Atitlán, 1,000 m, *Steyermark 47958* (US). HAITI. Massif de la Selle, Grand-Cosier, *Ekman 6856* (G). HONDURAS. COMAYAGUA: Zacate, La Libertad, *Caballero 124* (MO). COPAN: Hacienda Espíritu Santo, *Blake 7436* (US). EL PARAISO: Las Casitas, *Swallen 11075* (US). FRANCISCO MORAZAN: Mt. Uyuca, near Zamorano, 1,500 m, *McKee 11293* (US). OCOTEPEQUE: ca. 8 km SW of Santa Fe, near Guatemala border, *Williams et al. 31265* (MO). OLANCHO: Mata de Tarro, cerca de 18 km NE de Pisijire, *Nelson & Clewell 656* (MO). JAMAICA. Abbey Green, in the Blue Mountains, 1,200 m, *Hitchcock s.n., Amer. Gr. Hb. 133* (P, US, W). MEXICO. CHIAPAS: Mun. Las Margaritas, near albergue Tziscao, along W side of Lago Tizscao, 1,450 m, *Davidse et al. 29845* (MO). TABASCO: near the 21 km post W of Huimanguillo on the Huimanguillo–Francisco Rueda road, *Davidse & Davidse 9368* (MO). NICARAGUA. CHONTALES: along road from Jutigalpa NE toward La Libertad, ca. 17.4 km NE of Río Mayales, at ford of Río El Bizcocho, *Stevens 4118* (MO). ZELAYA: Puerto Isabel, *Atwood 2941* (MO). PANAMA. CHIRIQUI: El Boquete, *Killip 4525a* (US), *Davidson 766* (MO). PUERTO RICO. Maricao, *Sintenis 355* (G, M, US, W). UNITED STATES. ARKANSAS: Clark County, *Demaree 66629* (MO). MARYLAND: Without locality, *Zuloaga 2490** (SI). MISSOURI: Franklin County, Shaw Arboretum of the Missouri Botanical Garden, near Gray's Summit, *Davidse & Ellis 30807*, 30825** (MO). VIRGINIA: Alexandria, *Zuloaga 2492** (SI). VENEZUELA. ARAGUA: Colonia Tovar, 1,900 m, *Pittier 9962* (VEN). DISTRITO FEDERAL: Sabanas de El Junquito, 2,000 m, *Pittier 13773* (VEN). MIRANDA/DISTRITO FEDERAL: Campamento Las Rocas, below Topo Galindo, W of Pico Naiguata, Cordillera de la costa, *Tillett et al. 27* (VEN). MERIDA: 7 km SE of Santo Domingo along Mérida–Barinas highway, 1,700 m, *Davidse 3201* (MO). TRUJILLO: La Cristina, *Tamayo 1861* (US, VEN).

FIGURE 32. Distribution of *Panicum sabulorum* var. *cordatum*, *P. sabulorum* var. *polycladum*, and *P. sabulorum* var. *sabulorum*.

A sample of five specimens from both North America and South America was studied anatomically. The anatomical variation exhibited by the specimens originating from either continent is no greater than the variation observed between specimens from the same continent. The transectional anatomy clearly shows this trend. Only two of the specimens from the United States have a slightly differentiated midrib (Fig. 3A), whereas the other two North American specimens, as well as the South American specimens, all only have median vascular bundles (Fig. 2A). The semiradiate nature of the chlorenchyma tissue arrangement and bundle sheath extensions are consistent features of all the specimens.

*Panicum acuminatum* is the only species studied in which the anatomy of the basal rosette leaves was compared with that of the upper culm leaves. This comparison indicates that the rosette leaves lack adaxial ribs and furrows and have a denser mesophyll than the upper leaves (Fig. 4).

**2b. Panicum acuminatum** var. **longiligulatum** (Nash) Lelong, Brittonia 36: 270. 1984. *Panicum longiligulatum* Nash, Bull. Torrey Bot. Club 26: 574. 1899. *Dichanthelium acuminatum* (Sw.) Gould & Clark var. *longiligulatum* (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1127. 1978. *Dichanthelium longiligulatum* (Nash) Freckmann, Phytologia 48: 102. 1981. TYPE: United States. Florida: Franklin Co., Apalachicola, anno 1892, *Vasey s.n.* (holotype, NY; photo and fragment, US 78339). Figure 26.

*Panicum leucothrix* Nash, Bull. Torrey Bot. Club 24: 41. 1897. *Panicum acuminatum* Sw. var. *leucothrix* (Nash) Lelong, Brittonia 36: 271. 1984. *Dichanthelium leucothrix* (Nash) Freckmann, Phy-

tologia 58: 101. 1981. TYPE: United States. Florida: Lake Co., near Eustis, July 1894, *Nash 1338* (holotype, NY; isotypes, US 208336, 742828, 742830).

*Panicum wrightianum* Scribner, U.S.D.A. Div. Agrost. Circ. 11: 44. 1898. *Dichanthelium acuminatum* (Sw.) Gould & Clark var. *wrightianum* (Scribner) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1126. 1978. *Dichanthelium wrightianum* (Scribner) Freckmann, Phytologia 48: 101. 1981. TYPE: Cuba. Without locality, *Wright 3463* (holotype, US 2808947; isotype, G).

*Panicum pilatum* Swallen, Fieldiana, Bot. 28: 26. 1951. TYPE: Venezuela. Sucre: Cerro Turimiquire, rocky sandstone summit of E peak, 2,500 m, 6 May 1945, *Steyermark 62606* (holotype, US 1911673; isotypes, F, NY).

*Distribution and ecology:* United States, Mexico, the West Indies, Mesoamerica, Colombia, and Venezuela, 0–2,500 m, in open, wet savannas on sandy soils and forest edges.

*Selected specimens cited.* BELIZE. BELIZE: ca. 6 km N of Sand Hill along the old Northern Highway to Maskall, *Davidse & Brant 32844* (MO). CAYO: Mountain Pine Ridge, Baldy Beacon and vicinity, *Davidse & Brant 33069* (MO, SI). STANN CREEK: in pine ridge, Commerce Bight Pine Ridge, *Gentle 8170* (US). TOLEDO: savanna between the foothills of the Maya mountains at Chun Bank and the Southern Highway, *Davidse & Brant 32452* (MO, SI). COLOMBIA. SANTANDER: Mesa de los Santos, 1,500 m, *Killip & Smith 15193* (MO, US). CUBA. ISLA DE LA JUVENTUD: Santa Bárbara, white-sand savannas, *Alain & Killip 2108* (US). PINAR DEL RIO: Arroyo Mántua, *Ekman 10937* (G, US). DOMINICAN REPUBLIC. Cordillera Central, Prov. de Samana, Sabana de la Mar, *Ekman 15636* (G, US). HONDURAS. GRACIAS A DIOS: alrededores de Puerto Lempira, *Gorgun 18* (MO). MEXICO. CHIAPAS: Mun. Ocosingo, a 16 km al NW de Boca Lacantum, camino a Palenque, *Martínez 16348* (MO). NICARAGUA. Comarca del Cabo, Puente Pozo Azul, *Seymour 4576, 4741, 4743* (MO). ZELAYA: Puerto Cabezas, *Svenson 4486* (MO, SI). VENEZUELA. ANZOATEGUI: Distrito Libertad, ridges and tops of Montañas Negras, along the Sucre and Anzoátegui border, 20 airline km NE of Bergantín, NE of Buenos Aires, Serranía de Turimiquire, *Davidse & González 19537, 19611* (MO, SI). LARA: Dtto. Morán, hacia las "filas de las vacas," 1 km del caserío La Peña a 16.5 km de Humocaro Alto, *Burandt Jr. V0383* (MO).

**2c. Panicum acuminatum** var. **villosum** (A. Gray) Beetle, Phytologia 48: 192. 1981. *Panicum nitidum* Lam. var. *villosum* A. Gray, N. Amer. Gram. & Cyp. 2: 111. 1835. *Dichanthelium acuminatum* (Sw.) Gould & Clark var. *villosum* (A. Gray) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1124. 1978. *Panicum ovale* Elliott var. *villosum* (A. Gray) Lelong, Brittonia 36: 272. 1984. TYPE: United States. New York: Ontario Co., without locality, *Sartwell s.n.* (isotype, MO).

*Panicum villosissimum* Nash, Bull. Torrey Bot. Club 23: 149. 1896. TYPE: United States. Georgia: Bibb Co., Ocmulgee River, swamp below Macon, 18–24 May 1895, *Small s.n.* (holotype, NY; isotypes, NY, US).

*Panicum pseudopubescens* Nash, Bull. Torrey Bot. Club 26: 577. 1899. TYPE: United States. Alabama: Lee Co., Auburn, 7 May 1898, *Earle & Baker 1537* (holotype, NY; isotype, US).

*Distribution and ecology:* widespread in the eastern United States; also in Mexico, Honduras, Guatemala, and Nicaragua, in forests up to 2,500 m.

*Selected specimens cited.* GUATEMALA. CHIMALTENANGO: near Río Pixcayó, between Chimaltenango and San Martín Jilotepeque, *Standley 64360* (F). HUEHUETENANGO: around Laguna de Ocubilá, E of Huehuetenango, 1,900 m, *Standley 82760* (F, US). HONDURAS. FRANCISCO MORAZAN: vicinity of Suyapa, 1,200 m, *Swallen 11287* (MO). MEXICO. CHIAPAS: Mun. Teopisca, marsh near Teopisca, 1,800 m, *Breedlove & Davidse 54820* (MO). OAXACA: ca. 11 mi. SW of Sola de Vega along the road to Puerto Escondido, pine-oak forest on mountain slope, 2,080 m, *Davidse & Davidse 9688* (MO). SAN LUIS POTOSI: San Luis Potosí, *Schaffner 146* (NY). NICARAGUA. ESTELI: along new road from Hwy. 1 (at km 135.5 and ca. 10.6 km W of bridge at La Trinidad) to San Nicolás, ca. 9.5 km from Hwy. 1, 1,200–1,400 m; pine-oak forest, *Stevens & Montiel 14796, 17972* (MO). NUEVO SEGOVIA: 3 km N of Dipilto, pine forest on steep hills, 900 m, *Pohl & Davidse 12199* (MO).

**3. Panicum adenorhachis** Zuloaga & Morrone, Ann. Missouri Bot. Gard. 78: 154. 1991. TYPE: Brazil. Bahia: Mun. Rio de Contas, 6–10 km ao NO de Rio de Contas, na estrada para o Pico das Almas, 13°32′S, 41°53′W, 1,000 m, 21 July 1979, *Mori, King, dos Santos & Hage 12451a* (holotype, CEPEC; isotypes, MO, US). Figure 25.

Plants perennial; *culms* trailing, leaning over vegetation, many-noded, sparingly branched, internodes cylindric, hollow, glabrous, nodes brownish, short-pilose or glabrous. *Sheaths* striate, caducous, glabrous, covered with small glands, the margins long-ciliate; collar short-pilose. *Ligule* 0.2–0.6 mm long, a ciliate membrane. *Blades* narrowly lanceolate, 4–6 cm long, 0.3–0.5 cm wide, flat, subcordate, the adaxial surface scabrous, the abaxial surface glabrous and covered with small glands; margins long-ciliate with tuberculate hairs near base, otherwise scabrous. *Inflorescence* terminal, a lax, diffuse panicle 5–7 cm long, 4–5 cm wide, few-flowered; *main axis* flexuous and glandular, the nodes distant; first-order branches widely divergent, solitary at each node with scabrous and glandular axes and long-pilose axils; spikelets solitary and widely spaced; pedicels claviform, short-pilose. Axillary panicles similar to the terminal one. *Spikelets* narrowly ellipsoid, 2.7–3 mm long, 0.9 mm

wide, upper glume and lower lemma short-hispid and subequal, without a stipe between the lower and upper glume. *Lower glume* 0.7–0.8 mm long, less than ⅓ the length of the spikelet, acuminate, nerveless or 1-nerved, hyaline. *Upper glume* 9-nerved. *Lower lemma* 9-nerved. *Lower palea* lanceolate, 1.8 mm long, 0.4 mm wide, hyaline, ciliolate on the margins; lower flower absent. *Upper anthecium* narrowly ellipsoid, 2.3 mm long, 0.8 mm wide, stramineous, brownish at maturity, papillose with simple papillae in longitudinal rows; lemma short-mucronate and with small microhairs at the apex; rachilla prolonged beyond the upper anthecium as a short mucro. *Caryopsis* ellipsoid, brownish, 1.5 mm long, 0.7 mm wide; hilum punctiform, embryo less than half the length of the caryopsis.

*Distribution and ecology:* known only from Pico das Almas in Bahia, Brazil, growing in campos rupestres on rocky, humid soils, 1,000–1,850 m.

*Additional specimens examined.* BRAZIL. BAHIA: Alto do Pico das Almas, 1,850 m, 20 Feb. 1987, *Harley et al. 24460* (K); Mun. Rio de Contas, Pico das Almas, Vertente leste, subida do pico do Campo do Queiros, 13°32′S, 41°58′W, *Harley et al. 26437* (K, MO, SI).

Affinities of *P. adenorhachis* are discussed in Zuloaga & Morrone (1991).

**4. Panicum aequivaginatum** Swallen, Contr. U.S. Natl. Herb. 29: 271. 1949. TYPE: Brazil. Bahia: between Bom Gosto e Olivença, 15 Mar. 1943, *Fróes 19950* (holotype, US 1910768; photo of the holotype, K; isotype, US 2146782). Figures 5, 24B, 25.

*Panicum appressifolium* Swallen, Mem. New York Bot. Gard. 9: 258. 1957. TYPE: Guyana. Samwaraknatipu (Holi-tipu), Kamarang River, Wenamu Trail, 1,100 m, 10 Nov. 1951, *Maguire & Fanshawe 32564* (holotype, F 1449017; isotypes, K, NY, P, RB).

*Panicum belmonte* Renvoize, Kew Bull. 37: 325. 1982. TYPE: Brazil. Bahia: 24 km SW of Belmonte, on road to Itapebí, 24 Mar. 1974, *Harley et al. 17383* (holotype, CEPEC 10051; isotypes, K, MO, US 2955112).

*Panicum thinophilum* Renvoize, Kew Bull. 39: 180. 1984. TYPE: Brazil. Bahia: Mun. Salvador, Dunas do Abaeté, 17 Dec. 1976, *Araujo et al. 96* (holotype, CEPEC; isotypes, CEN, K).

Apparently annual, 20–100 cm tall. *Culms* decumbent, rooting and branching at the lower nodes, then erect; internodes hollow, 3.5–10.5 cm long, short-hispid or glabrous, nodes compressed, pilose with appressed whitish hairs. *Sheaths* 3–8.5 cm long, usually shorter than the internodes, hispid or glabrous, striate, the margins ciliate. *Ligules* 0.3–0.6 mm long, membranous, the apex ciliate; collar pilose with whitish hairs. *Blades* linear-lanceolate, 3.5–12 cm long, 0.5–1.3 cm wide, ascendent, hispid or glabrous, long-pilose toward the base on the adaxial surface, cordate to subcordate, acute, the margins scaberulous and ciliate, the midnerve conspicuous. *Inflorescences* exserted, a terminal, lax and diffuse panicle 10–15 cm long, 3–7 cm wide; *main axis* glabrous, flexuous, smooth, the pulvini short-pilose or glabrous, first-order branches alternate, divergent from the main axis and flexuous, pedicels smooth and glabrous, flexuous. *Spikelets* paired or solitary, ellipsoid, 1.7–2.5 mm long, 0.7 mm wide, glabrous, with a short, inconspicuous internode between the lower and upper glume. *Lower glume* ovate-acuminate, 0.9–1.3 mm long, ½ or less the length of the spikelet, glabrous, not embracing the upper glume, 3-nerved, the nerves either anastomosing or not toward the apex. *Upper glume* usually not covering the apex of the upper anthecium, 9-nerved, the nerves anastomosing or not toward the apex. *Lower lemma* glumiform, 9-nerved. *Lower palea* linear-lanceolate, small, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 1.6–1.9 mm long, 0.6 mm wide, with simple papillae, apiculate; stigmas whitish. *Caryopsis* ellipsoid, brownish, hilum punctiform, embryo ⅓ or less the length of the caryopsis.

*Distribution and ecology:* occurring in Venezuela, in the states of Bolívar and Amazonas, Guyana, and northern Brazil, from 900 to 2,000 m. Frequent in savannas or mountain slopes, in sandy soils in Venezuela; in Brazil it grows in sandy soils of campos rupestres and restingas.

*Additional specimens examined.* BRAZIL. BAHIA: El Salvador, coastal dunes 2 km N of town of Itapua, near sea level, *Plowman & Almeida 10045* (CEPEC, MO, US); Estrada de Bom Gosto a Olivença, *Fróes 19950* (US); Lençois, along BR 242, ca. 15 km NW of Lençois at km 225, *Mori & Boom 14257* (CEPEC, MO); camino de Maraú a Ubaitaba, 15 km de Maraú, *Zuloaga et al. 2469** (MO, RB, SI, US); margen da Rodovia Camacã-Canavieiras, 32 km W de Canavieiras, *Belém 1692* (CEPEC, IAN, NY, SI, UB, US); rodovia Brasília–Fortaleza, BR-242, 8 km da estrada para Lençois, campo rupestre, *Coradin et al. 6530* (CEN, K, MO, SP). RIO DE JANEIRO: restinga de Jacarepaguá, do lado NW da Pedra de Itaúna, *Sucre 5349* (RB, SI); Guanabara, estrada BR-6, *Hoehne 5991* (SI, SP); Rio de Janeiro, próximo ao Recreio dos Bandeirantes, *Hoehne 5789* (SI, SP). RORAIMA: Mt. Roraima, Philipps Camp, 5,200–6,000 ft., *Tate 281* (NY, US). GUYANA. Pakaraima Mountains, Mt. Aymatoi, *Maas et al. 5769* (K, MO, NY, US). VENEZUELA. AMAZONAS: Cerro de la Neblina, Río Yatua, along Cañón Grande E of Cumbre Camp, 1,100 m, *Maguire et al. 42193* (NY, P, US, VEN). BOLIVAR: La Gran Sabana, km 167, S of El Dorado along highway to Santa Elena, 24 km S of La

Ciudadela, *Davidse 4762* (MO, SI, VEN); la Gran Sabana, a 2 km al sur de La Ciudadela, 5°47′N, 61°25′W, 1,300 m, *Zuloaga et al. 4408* (MO, SI, VEN); a 3 km al N de Kamoirán, Gran Sabana, 5°35′N, 61°20′W, 1,100 m, *Zuloaga et al. 4470** (MO, SI, VEN); Uaipán-tepui, near the top of Salto Hacha on plateau at S foot of the peak of Uaipán, *Koyama & Agostini 7391* (VEN); Mun. Gran Sabana, inmediaciones del Monumento al Soldado Pionero, 38.5 km al S del sitio "Piedra de la Virgen," *Huber et al. 12908* (MYF, SI).

This species is related to *P. pycnoclados* and *P. sciurotoides*, but has spikelets intermediate in size between both species. It also differs from *P. sciurotoides* in that the latter species has cordate and amplexicaulous leaves, the main inflorescence axis hirsute, and usually pilose spikelets. *Panicum pycnoclados* differs from *P. aequivaginatum* by its cordate and amplexicaulous, asymmetrical leaf blades, smaller inflorescences, 3–6(–10) cm long, spikelets 2.2–3(–3.3) mm long with a conspicuous internode between the lower and upper glume; lower glume ½–¾ the length of the spikelet.

*Panicum thinophilum* only represents a depauperate variant of *P. aequivaginatum* with profusely branching culms and axillary panicles.

**5. Panicum assurgens** Renvoize, Kew Bull. 37: 325. 1982. TYPE: Brazil. Bahia: on road to Abaira, ca. 8 km to N of the town of Rio de Contas, 13°33′S, 41°47′W, 1,000 m, 18 Jan. 1972, *Harley et al. 15229* (holotype, CEPEC; isotypes, K, MO, NY, US 2955120). Figures 24A, 25.

Probably perennial. *Culms* leaning on adjacent vegetation, to 2 m long, internodes 4–10 cm long, cylindric, glabrous; nodes glabrous, compressed. *Sheaths* 3–7 cm long, shorter than the internodes, striate, sparsely hispid, with one margin ciliate, the other glabrous. *Ligules* membranous, the membranous portion 0.2 mm long, short-pilose at the apex with hairs nearly 0.1 mm long; collar shortly pilose. *Blades* linear-lanceolate, 8–12 cm long, 0.7–1 cm wide, flat, sparsely hispid, attenuate at base and with the apex acute, the margins finely scabrous. *Inflorescences* terminal, long-exserted, lax, diffuse, 12–15 cm long, 7–10 cm wide, first-order branches whorled toward the base of the inflorescence, otherwise subopposite or alternate, axis of the branches flexuous, glabrous, eglandular, pulvini glabrous, pedicels glabrous. *Spikelets* ellipsoid, 3.3 mm long, 1.2 mm wide, glabrous or sparsely pilose between the nerves, greenish, without a conspicuous internode between the lower and upper glume, upper glume and lower lemma subequal. *Lower glume* ovate-lanceolate, 2.1–2.7 mm long, ¾–⅘ the length of the spikelet, not embracing the upper glume at its base, glabrous, 3-nerved, the nerves anastomosing toward the apex. *Upper glume* 2.7 mm long, as long as the lower lemma or a little shorter and not covering the apex of the upper anthecium, 9-nerved. *Lower lemma* 9-nerved, 2.7–2.9 mm long. *Lower palea* lanceolate, 2 mm long, 0.3 mm wide, hyaline, sparsely pilose; lower flower absent. *Upper anthecium* ellipsoid, 2.7 mm long, 1 mm wide, papillose, upper lemma slightly apiculate, the upper margins indurate, sparsely pilose at the apex. *Caryopsis* ellipsoid, 2.1 mm long, 0.9 mm wide; hilum punctiform, embryo ⅓ or less the length of the caryopsis.

*Distribution and ecology:* known only from the type collection, where it grows at edges of forests in the state of Bahia, Brazil, at approximately 1,000 m.

**6. Panicum cabrerae** Zuloaga & Morrone, Ann. Missouri Bot. Gard. 78: 156. 1991. TYPE: Brazil. Bahia: Mun. Rio de Contas, Pico das Almas, a 18 km ao SNW de Rio de Contas, 13°33′S, 41°57′W, 1,600–1,850 m, 22 July 1979, *Mori, King, dos Santos & Hage 12475* (holotype, CEPEC; isotypes, MO, US). Figure 26.

Perennial. *Culms* ca. 50 cm tall, leaning on vegetation, sparingly branching, internodes cylindric, hollow, sparsely pilose with whitish hairs, nodes many, densely pilose with long whitish hairs. *Sheaths* striate, 1.5–2 cm long, longer than the internodes, long-hispid, the margins pilose with whitish hairs, more so toward the upper portion; auricles small, pilose; collar pilose. *Ligules* ciliate-membranous ca. 0.2 mm long. *Blades* linear-lanceolate, 4–6 cm long, 2 mm wide, attenuate at base, acuminate at apex, the margins involute, densely pilose and scabrous, with long, whitish hairs on both surfaces, deciduous at maturity. *Inflorescence* terminal, a lax, diffuse panicle 4.5–6 cm long, 3.5–6 cm wide, peduncles hispid, 5–7 cm long; *main axis* cylindric, densely hispid on the lower portion, otherwise glabrous, the nodes distant; first-order branches alternate, divergent and reflexed, hispid basally, glabrous distally, pulvini pilose to glabrous; pedicels claviform, smooth, glabrous, 2–9 mm long. *Spikelets* solitary, ellipsoid, 2–2.3 mm long, 0.8–0.9 mm wide, plano-convex, hirsute, with whitish hairs on the glumes and lower lemma. *Lower glume* 1.1–1.3 mm long, ½ or more the length of the spikelet, 3-nerved, acute, a small stipe present between the lower and upper glume. *Upper glume* 9-nerved, nerves anastomosing toward the apex.

*Lower lemma* 9-nerved. *Lower palea* lanceolate, 1.5–1.8 mm long, 0.3 mm wide, glabrous, truncate, hyaline; lower flower absent. *Upper anthecium* ellipsoid, 1.9 mm long, 0.7 mm wide, papillose, with simple papillae all over its surface, glabrous or with a few microhairs toward the apiculate apex; lodicules truncate, ca. 0.2 mm long, anthers 3, 1.2 mm long; rachilla prolonged or not beyond the upper anthecium as a short mucro. *Caryopsis* obovoid, 1.1 mm long; hilum oblong, embryo less than ⅓ the length of the caryopsis.

*Distribution and ecology:* growing in campos rupestres, in the state of Bahia, Brazil.

*Additional specimens examined.* BRAZIL. BAHIA: Mun. Rio de Contas, Pico das Almas, vertente leste, subida do pico do campo N do Queiroz, 13°32′S, 41°58′W, 1,600 m, *Harley, Giulietti, Stannard & Hind 26320* (K).

*Panicum cabrerae* shares with *P. aciculare* a similar vegetative pattern, with linear, pilose blades, small panicles and spikelets of more or less the same size. *Panicum cabrerae* differs from *P. aciculare* in that the latter species has obovoid spikelets with the upper glume and lower lemma 7-nerved, and the lower palea absent; also, *P. aciculare* is found from the southern United States to Colombia and Venezuela.

7. **Panicum caparaoense** Zuloaga & Morrone, sp. nov. TYPE: Brazil. Espírito Santo: Mun. Muñiz Freire, Rodovia BR-262, 1,000 m, 21 July 1982, *Hatschbach & Guimaraes 45170* (holotype, K; isotype, MBM not seen). Figure 36.

Ligula membranacea 0.8 mm longa; lamina lanceolata 14–21 cm longa, 1 cm lata, complanata; paniculae laxae, diffusae, 23 cm longae; spiculae modice ellipsoideae, 5.9–6.8 mm longae, glabrae; gluma inferior ⅔ spiculae longitudine, acuminata, 5-nervia; gluma superior 13–15 nervia; lemma inferius 13–15-nervium, palea inferior lanceolata, 5.5 mm longa, 1.2 mm lata, margine longe pilosa; anthoecium longe ellipsoideum, 5.2 mm longum, 1.6 mm latum, papillis simplicibus praeditum, necnon lemmate marginibus superioribus cristato ac piloso.

Plants perennial?, the base not seen; internodes hollow, cylindric, glabrous, nodes dark, compressed, glabrous. *Sheaths* striate, one margin ciliate, otherwise glabrous. *Ligules* membranous at the base and laciniate at the apex, 0.8 mm long, brownish, surmounted by long whitish hairs on the adaxial surface of the blade; collar densely and shortly pilose. *Blades* lanceolate, 14–21 cm long, 1 cm wide, flat, attenuate at the base and apex, the adaxial surface with scattered, appressed hairs, the abaxial surface glabrous, commonly purplish, the margins ciliate. *Inflorescence* terminal, exserted, peduncle terete, ca. 22 cm long, glabrous; panicles lax, diffuse, 23 cm long, ca. 20 cm wide; *main axis* terete, glabrous, the pulvini brownish, glabrous; first-order branches alternate, divergent, the axis of the branches and pedicels smooth, glabrous. *Spikelets* solitary, narrowly ellipsoid, 5.9–6.8 mm long, glabrous. *Lower glume* 4.1 mm long, ⅔ the length of the spikelet, acuminate, 5-nerved, separated from the upper glume by a conspicuous internode. *Upper glume* scaberulous toward the apex, 13–15-nerved, the nerves anastomosing toward the apex. *Lower lemma* scaberulous toward the apex, 13–15-nerved, the nerves anastomosing toward the apex. *Lower palea* lanceolate, 5.5 mm long, 1.2 mm wide, hyaline, the margins long-pilose with whitish hairs; lower flower male, anthers ca. 3 mm long. *Upper anthecium* narrowly ellipsoid, 5.2 mm long, 1.6 mm wide, smooth, shiny, indurate, with simple papillae regularly distributed over the lemma and palea, lemma 9-nerved, crested and pilose on the upper margins, greenish at the apex, palea pilose on the upper margins; lodicules 2, conduplicate, 0.4 mm long; stamens 3, the anthers 3 mm long; styles free, stigma plumose; rachilla prolonged beyond the upper anthecium as a short mucro. *Caryopsis* unknown.

*Distribution and ecology:* known from the state of Espírito Santo in Brazil, where it grows in edge of forests.

*Paratype.* BRAZIL. ESPIRITO SANTO: Castelo, Braço do Sul, *Brade 19172* (US).

*Panicum caparaoense* is related to *P. itatiaiae* and *P. davidsei*. *Panicum itatiaiae* has spikelets 4.6–5 mm long, the lower palea glabrous or sparsely pilose, and the leaf blades subcordate. *Panicum davidsei* has spikelets 3–3.3 mm, lower flower absent, and upper anthecium glabrous or shortly pilose.

The specific epithet makes reference to the type locality of this new species, the Serra do Caparaó in Espírito Santo, Brazil.

8. **Panicum congestum** Renvoize, Kew Bull. 37: 329. 1984. TYPE: Brazil. Bahia: 22 km NW of Lagoinha, which is 5.5 km SW of Delfino, on side road to Minas do Mimoso, 980 m, 6 Mar. 1974, *Harley, Renvoize, Erskine, Brighton & Pinheiro 16869* (holotype, CEPEC 10082; isotypes, K, MO, NY, RB, US 2955113). Figure 25.

Caespitose perennial. *Culms* erect, freely branching at the upper nodes, 30–50 cm tall, rigid;

internodes elongated toward the base of the plant, terete, hollow, densely hirsute, nodes brownish, pilose. *Sheaths* persistent or deciduous, striate, densely hirsute, the margins membranous. *Ligules* membranous-ciliate, ca. 1 mm long, with whitish hairs; collar pilose. *Blades* linear-lanceolate, 1.5–5 cm long, 0.2–0.4 cm wide, congested on the culms, the margins involute, narrowed at base and acuminate at the apex, densely hirsute on both surfaces with rigid whitish hairs. *Inflorescences* with base included within the upper leaves, with a peduncle ca. 0.5 cm long; panicles 2 cm long or smaller, contracted, with only 2–3(–9) spikelets per panicle; *main axis* hirsute, flexuous, first-order branches short, the axis of the branches and pedicels densely hirsute. *Spikelets* solitary, ellipsoid, 2.8–3.2 mm long, 1 mm wide, hirsute, with short-papillose hairs, upper glume and lower lemma subequal or the upper glume a little shorter. *Lower glume* 2.2–2.6 mm long, ¾ or more the length of the spikelet, acute, 5–7-nerved, the nerves anastomosing toward the apex, with a conspicuous internode between the lower and upper glume. *Upper glume* 2.6 mm long, 9-nerved. *Lower lemma* 9-nerved, glumiform. *Lower palea* lanceolate, 1.7 mm long, 0.4 mm wide, hyaline, the margins ciliolate; lower flower absent. *Upper anthecium* ellipsoid, 2.4 mm long, 0.8 mm wide, papillose, with simple papillae regularly distributed over the lemma and palea, apiculate and pilose at the tip of the lemma, lemma 5-nerved; internodes conspicuous between the upper glume and the upper anthecium. *Caryopsis* ellipsoid, brownish, hilum oblong, embryo ⅓ the length of the caryopsis.

*Distribution and ecology:* known only from campos rupestres in the state of Bahia, Brazil, where it is found on sandstone rocks at approximately 1,000 m.

This species is distinguished by its densely hirsute and profusely branching culms, hirsute sheaths and blades, and few-flowered inflorescences that are short-exserted with the base included in the upper leaves.

**9. Panicum cucaense** Zuloaga & Morrone, Ann. Missouri Bot. Gard. 78: 158. 1991. TYPE: Brazil. Rio de Janeiro: Mun. Petrópolis, Morro do Cuca, entre Vale dos Videiras e Araras, campo de altitude, 1,600 m, 27 Jan. 1983, *Martinelli & Simonis 9011* (holotype, RB; isotypes, MO, SI). Figure 27.

Caespitose, shortly rhizomatous perennial. *Culms* 20–30 cm tall, many-noded, erect to geniculate-ascending and rooting at the lower nodes, freely branching; internodes 1–4 cm long, cylindric, striate, glabrous; nodes compressed, glabrous, brownish. *Sheaths* striate, ca. 1.2 cm long, longer than the internodes, strongly distichous, long-pilose on the distal portion, otherwise glabrous, one margin pilose with long, whitish hairs, the other one membranous. *Ligule* ciliate-membranous, the membranous portion ca. 0.1 mm long, the ciliate portion 0.4 mm long. *Blades* linear, 1.5–5.5 cm long, 0.1–0.2 cm wide, folded, attenuate toward the apex, pilose on the adaxial surface toward the ligule, otherwise glabrous, the borders scabrous. *Primary inflorescences* lax, diffuse, few-flowered, 2–3.5 cm long, 1.5–3.5 cm wide; peduncles to 6 cm long, glabrous; *main axis* striate, flexuous, glabrous, somewhat glandular, the branches alternate, divergent and widely spaced, glabrous, the axils of the branches pilose; pedicels glabrous, 1–6 mm long. *Secondary inflorescences* similar to the terminal one. *Spikelets* ellipsoid, 2.2–2.7 mm long, 0.8–0.9 mm wide, gaping at maturity, glabrous. *Lower glume* lanceolate, 1.5–1.9 mm long, ⅔–¾ the length of the spikelet, acuminate, 1(–3)-nerved, a small stipe present between the lower and upper glume. *Upper glume* and *lower lemma* subequal, 7–9-nerved, acute. *Lower palea* lanceolate, 1.7–1.9 mm long, 0.4–0.7 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* narrowly ellipsoid, 2.1–2.3 mm long, 0.7–0.8 mm wide, papillose, with simple papillae evenly distributed over the lemma and palea, apiculate, the apex scabrous, otherwise glabrous; lodicules ca. 0.2 mm long; stamens 3, anthers 1.2 mm long. *Caryopsis* ellipsoid, 1.4 mm long, 0.7 mm wide, brownish; hilum oblong; embryo less than half the length of the caryopsis.

*Distribution and ecology:* inhabiting open and dry habitats, in rocky, granitic soils of high-altitude campos of mountains in eastern Brazil, at 2,000–2,500 m.

*Additional specimens examined.* BRAZIL. RIO DE JANEIRO: Teresópolis, Serra dos Orgãos, Pedra do Sino, 2,100–2,170 m, Feb. 1953, *J. Vidal II-6467, II-6485* (R, SI); Mun. Petrópolis, Vale das Videiras, Morro do Cuca, 1,800 m, 17 Apr. 1976, *Martinelli 814* (RB); without locality, *Glaziou 13319* (W).

Affinities of *P. adenorhachis* are discussed in Zuloaga & Morrone (1991).

**10. Panicum cumbucana** Renvoize, Kew Bull. 37: 332. 1982. TYPE: Brazil. Bahia: by Rio Cumbuca, 3 km S of Mucugê, near site of small dam on road to Cascavel, 850 m, 4 Feb. 1974, *Harley, Renvoize, Erskine, Brighton*

*& Pinheiro 15930* (holotype, CEPEC 10042; isotypes, K, MO, NY, US 2955114). Figures 24C, 27.

Short-rhizomatous perennial. *Culms* long decumbent, then erect, to 35 cm tall, freely branching at the upper nodes, internodes 1–2.8 cm long, hispid, hollow, nodes hispid. *Sheaths* 1–2 cm long, usually shorter than the internodes, hispid or glabrous, one margin long-ciliate, the other short-pilose. *Ligules* 0.4–0.6 mm long, shortly membranous at the base, ciliate at the apex, arcuate; collar shortly pilose. *Blades* lanceolate, 1–3 cm long, 0.3–0.6 cm wide, rigid, ascending and slightly divergent from the culms, cordate and amplexicaulous, acute, glabrous or shortly and densely hispid on both surfaces, with or without long hairs toward the base on the adaxial surface, the margins scaberulous, long-ciliate toward the base of the blades, the midnerve inconspicuous. *Inflorescences* exserted or with the base included within the upper leaves, panicles lax, few-flowered, 1–2.5(–3) cm long, 1–2 cm wide; *main axis* hispid to sparsely pilose, first- and second-order branches shortly pilose, divergent, eglandular, the pulvini pilose; pedicels sparsely pilose. *Spikelets* solitary or paired, ellipsoid, 1.9–2.4 mm long, 0.6–0.8 mm wide, shortly hispid or glabrous, upper glume and lower lemma subequal. *Lower glume* ovate, 1–1.3 mm long, 0.9 mm wide, ½ the length of the spikelet, pilose or glabrous, not embracing the upper glume at its base, (1–)3-nerved, with a conspicuous internode ca. 0.3 mm long between the lower and upper glume. *Upper glume* 1.5–1.9 mm long, pilose, 7–9-nerved, usually not covering the apex of the upper anthecium. *Lower lemma* 1.5–1.9 mm long, glumiform. *Lower palea* linear-lanceolate, 1.2–1.5 mm long, 0.2–0.3 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 1.5–1.8 mm long, 0.5–0.7 mm wide, pale, indurate, papillose, and pilose; lemma 5-nerved, palea 2-nerved, anthers 0.9 mm long, purplish. *Caryopsis* ellipsoid, 1.2–1.5 mm long, 0.2–0.3 mm wide; hilum punctiform, embryo less than ½ the length of the caryopsis.

*Distribution and ecology:* found in campos rupestres in the state of Bahia, Brazil, in sandy, rocky soils from 900 to 1,400 m.

*Additional specimens examined.* BRAZIL. BAHIA: 10 km NW of Mucugê, *Mori et al. 12698* (CEPEC, MO, SI, US); Serra do Sincorá, 2–3 km approximately SW of Mucugê on the road to Cascavel, 950 m, *Harley et al. 18829* (CEPEC, MO, NY, US); Mucugê, Serra do Sincorá, 7 km N of Mucugê on road to Andaraí, growing in small patches under Velloziaceae and other plants, *Calderón et al. 2425** (SI, US); Mucugê, Serra do Sincorá, 26 km S of Andaraí, 1,000 m, on rocks, between mosses with water running over, *Calderón et al. 2414* (US); Mun. Mucugê, Rio Apiaba, *Hatschbach 48266* (CTES, K, US); Serra do Rio de Contas, lower N slopes of the Pico das Almas, ca. 25 km WNW of the town of Rio de Contas, *Harley et al. 15420* (CEPEC, K, NY, US); Mun. Mucugê, Rio Mucugê, *Hatschbach 47961* (K); Serra Larga a W de Lençóis, perto de Caeté–Açu, Mun. Lençóis, 1,400 m, 19 Dec. 1984, *Harley et al. s.n.* (K, MO); Mun. Jacobina, scrub and woodland with *Vellozia*, hills of marble rock on N side of Jacobina, 600–650 m, *Webster et al. 25725* (MO); estrada entre Andaraí–Mucugê, *Noblick & Pinto 2870* (K).

*Panicum cumbucana* is closely allied to, and perhaps conspecific with *P. stipiflorum*, which only differs by having leaf blades 2–4.5 cm long, usually not overlapping, and inflorescences 3–4.5 cm long. The culms and leaf blades are usually purplish in *P. cumbucana*, and the blades are, in many cases, overlapping.

Anatomically, the abaxial epidermis of *P. cumbucana* closely resembles that of *P. hebotes*, *P. peristypum*, and *P. sciurotoides* due to the numerous, needlelike macrohairs without cushion bases and because of the short, angular, intercostal cells, which resemble bulliform cells in surface view. However, in transverse section this resemblance is not so evident because *P. cumbucana* does not have well-developed adaxial ribs and furrows and lacks a keel (Fig. 6A, B).

**11. Panicum davidsei** Zuloaga & Morrone, Ann. Missouri Bot. Gard. 78: 158. 1991. TYPE: Venezuela. Bolívar: Cabanayén, La Gran Sabana, wet inundated savanna, 1,300, 3 Dec. 1973, *Davidse, Ramia & Montes 4796* (holotype, MO). Figures 7, 27.

Perennial. *Culms* decumbent, rooting and branching at the lower nodes, then becoming erect, leaning or not on vegetation, to 2.2 m long, internodes 8–22 cm long, cylindric, striate, hispid, compressed, nodes hirsute. *Sheaths* 5–8 cm long, sparsely hirsute with long-tuberculate hairs, one of the margins long-ciliate, the other one membranous; collar long-pilose with whitish hairs. *Ligules* membranous-ciliate, ca. 0.2 mm long. *Blades* narrowly lanceolate, 9–13 cm long, 1–1.3 cm wide, flat, subcordate, the apex acuminate, the adaxial surfaces long-pilose toward the base, otherwise glabrous, the abaxial surfaces sparsely pilose, the margins scabrous and ciliate toward the base, the midnerve conspicuous. *Inflorescence* terminal, long-exserted, a lax, diffuse panicle 12–20 cm long and 7–12 cm wide, peduncle 10–40 cm long; *main axis* cylindric, striate, pilose near the branches, otherwise glabrous, eglandular, lower branches

whorled, the upper ones subopposite to alternate, the axis of the branches flexuous, glabrous, eglandular, the pulvini pilose; pedicels glabrous, flexuous. *Spikelets* ellipsoid, 3–3.3 mm long, 1 mm wide, scaberulous, attenuate toward the base and with a small stipe between the lower and upper glume, upper glume and lower lemma subequal with manifest nerves. *Lower glume* ovate-acuminate, 1.5–1.8 mm long, nearly ½ the length of the spikelet, 3-nerved. *Upper glume* 2.4–2.7 mm long, not covering the apex of the upper anthecium, 11–14-nerved, the nerves anastomosing toward the apex. *Lower lemma* ca. 2.7 mm long, 10–12-nerved, the nerves anastomosing toward the apex. *Lower palea* lanceolate, 2.1–2.4 mm long, 0.3 mm wide, glabrous, hyaline; lower flower absent. *Upper anthecium* ellipsoid, 2.4–2.7 mm long, 1 mm wide, papillose, apiculate, the lemma with a green, scabrous crest on the apex and with the upper margins membranous, prolonged toward the apex as small wings; rachilla prolonged beyond the upper anthecium as a small mucro; lodicules ca. 0.4 mm long; stamens 3, anthers ca. 1.2 mm long. *Caryopsis* ellipsoid, 1.8 mm long, 0.9 mm wide, hilum punctiform, embryo ⅓ the length of the caryopsis.

*Distribution and ecology:* found in Bolívar Venezuela, and Roraima, Brazil, on forest edges (where it leans on the vegetation), or in open places in sandy soils, 1,200–1,300 m.

*Additional specimens examined.* BRAZIL. RORAIMA: Aldeia do Tuchana, *Rondôn s.n.*, July 1927 (RB 110786). VENEZUELA. BOLIVAR: entre piedra de La Virgen y la parte alta de la Escalera, carretera a la Gran Sabana, 6°00′N, 61°25′W, 1,300 m, *Zuloaga et al. 4406** (MO, SI, VEN); a 1 km al S del Puente Sakaika, Gran Sabana, 1,200 m, *Zuloaga et al. 4427** (MO, SI, VEN).

Affinities of *P. adenorhachis* are discussed in Zuloaga & Morrone (1991).

The large number of nerves in the upper glume and lower lemma of this new species suggests a relationship to *P. itatiaiae* and *P. caparaoense*, species from eastern Brazil with spikelets 4.6–6.8 mm long.

*Panicum davidsei* has a thick leaf blade without a midrib, well-developed adaxial ribs and furrows, and conspicuous, long bundle sheath extensions (due to the thickness of the lamina) (Fig. 7A–C).

**12. Panicum dichotomum** L., Sp. Pl.: 58. 1753. *Dichanthelium dichotomum* (L.) Gould, Brittonia 26: 59. 1974. TYPE: United States. Virginia: "Habitat in Virginia," *Clayton 458* (lectotype, BM not seen; photo and fragment, US 2808912).

Perennial. *Culms* decumbent, 10–25(–80) cm long, fasciculate and densely branching at the middle and upper nodes, internodes glabrous, cylindric, hollow, nodes glabrous or short-pilose. *Sheaths* glabrous, glandular or eglandular, the margins membranous, one margin long-ciliate. *Ligules* membranous-ciliate, 0.1–0.6 mm long; collar glabrous. *Blades* linear-lanceolate, 2–7 cm long, 0.2–0.5(1.2) cm wide, flat or slightly involute, glabrous to sparsely pilose, narrowed at the base, attenuate at the apex, the margins scaberulous, cartilaginous or not, usually ciliate toward the base, otherwise glabrous. *Inflorescences* terminal, short- to long-exserted, peduncle glabrous, 3–16 cm long; panicles 1–5 cm long, 1–3 cm wide, lax, few-flowered; *main axis* scabrous or glabrous, glandular or eglandular, the pulvini glabrous, first-order branches alternate, divergent, glandular or eglandular; pedicels flexuous, 2–9 mm long, scabrous or glabrous. Axillary panicles similar to the terminal one. *Spikelets* solitary, obovoid or ellipsoid, 1.4–2.3 mm long, 0.6–1 mm wide, glabrous or shortly hispid, greenish or tinged with purple, the upper glume and lower lemma subequal. *Lower glume* ovate, 0.3–0.7 mm long, ¼ to ⅓ the length of the spikelet, obtuse to truncate, glabrous, nerveless or 1-nerved. *Upper glume* 1.2–1.8 mm long, not covering the apex of the upper anthecium, 7-nerved, separated from the lower lemma by a short internode. *Lower lemma* 1.2–1.7 mm long, glumiform, 7-nerved. *Lower palea* lanceolate, small, 0.8–1 mm long, 0.3 mm wide, glabrous, hyaline; lower flower absent. *Upper anthecium* obovoid, 1.1–1.7 mm long, 0.7–1 mm wide, pale, indurate, acute, papillose, scaberulous toward the apex. *Caryopsis* obovoid, dark, 1.2 mm long, 0.8 mm wide; hilum punctiform, embryo less than ½ the length of the caryopsis.

KEY TO THE VARIETIES

1. Blades without cartilaginous margins; spikelets 1.8–2.3 mm long ..... 12a. var. *dichotomum*
1. Blades with cartilaginous margins; spikelets 1.4–1.6 mm long ..... 12b. var. *tenue*

**12a. Panicum dichotomum** var. **dichotomum**. Figure 27.

*Panicum nitidum* Lam., Tabl. Encycl. 1: 172. 1791. *Panicum dichotomum* L. var. *nitidum* (Lam.) Alph. Wood, Class-Book Bot., ed. 3: 786. 1861. TYPE: United States. "E. Carolina," *Fraser s.n.* (holotype, P-LAM; fragment and photo, US 80880).

*Panicum nodiflorum* Lam., Encycl. 4: 744. 1798. *Panicum dichotomum* L. var. *nodiflorum* (Lam.) Griseb., Cat. Pl. Cuba 234. 1866. TYPE: United States. South Carolina: without locality, *Fraser s.n.* (holotype, P-LAM; fragment and photo, US 2808963).

*Panicum barbulatum* Michaux, Fl. Bor. Amer. 1: 49. 1803. *Panicum dichotomum* L. var. *barbulatum* (Michaux) Alph. Wood, Class-Book Bot., ed. 3: 786. 1861. *Panicum pubescens* Lam. var. *barbulatum* (Michaux) Britton, Cat. Pl. New Jersey 280. 1889. *Panicum nitidum* Lam. var. *barbulatum* (Michaux) Chapman, Fl. South. U.S., ed. 3: 586. 1897. TYPE: Canada. "Hab. in Canada P. capillari affine. Ad ripas amnis: *Riviere* a Jacques Cartier dicti legi," *Michaux s.n.* (lectotype, P-MICH; fragment, US).

*Panicum maculatum* Ashe, J. Elisha Mitchell Sci. Soc. 15: 44. 1898, non Aublet 1775. *Panicum yadkinense* Ashe, J. Elisha Mitchell Sci. Soc. 16: 85. 1900. *Panicum dichotomum* L. var. *yadkinense* (Ashe) Lelong, Brittonia 36: 266. 1984. TYPE: United States. North Carolina: Wake Co., Raleigh, May 1895, *Ashe s.n.* (lectotype, US).

*Panicum roanokense* Ashe, J. Elisha Mitchell Sci. Soc. 15: 44. 1898. *Panicum dichotomum* L. var. *roanokense* (Ashe) Lelong, Brittonia 36: 265. 1984. TYPE: United States. North Carolina: Dare Co., Roanoke Island, June 1898, *Ashe s.n.* (lectotype, US).

*Panicum multirameum* Scribner, U.S.D.A. Div. Agrost. Circ. 19: 2. 1900. TYPE: Mexico. Veracruz: near Jalapa, 1889, *Pringle 7882* (lectotype, US 743295; isolectotype, MO).

*Panicum caerulescens* Hackel ex A. Hitchc., Contr. U.S. Natl. Herb. 12: 219. 1909. TYPE: United States. Florida: Dade Co., Miami, 3 Apr. 1906, *Hitchcock 706* (holotype, US; isotype, NY).

*Distribution and ecology:* common in North America, from Canada to Mexico, in moist ground, open swampy wood and wet meadows. In South America it is known from the Cerro Santa Ana, Falcón, Venezuela.

*Selected specimens cited.* CUBA. HABANA: Batabanó, *León 6152* (US). ISLA DE LA JUVENTUD: along road to Santa Isabel near SE base of Cerro Daguilla, sabanas, *Killip 44853* (US). ORIENTE: Sierra de Nipe, Loma Mensura, *León 19828* (US). SANTA CLARA: Sabana de San Marcos, *León 9203* (US). DOMINICAN REPUBLIC. AZUA: Sierra de Ocoa, San José de Ocoa, 1,550 m, *Ekman 11942* (US). LA VEGA: vicinity of Jarabacoa, 500–1,200 m, *Allard 14509a* (US). MONTE CRISTI: Cordillera Central, on the ridge between Río Cenobí and Río de la Cidra, 700 m, *Ekman 12697* (US). GUATEMALA. ALTA VERAPAZ: large swamp just E of Tactic, 1,300 m, *Steyermark 43942* (F, US). ZACAPA: between Loma El Picacho and Cerro de Monos, 2,000–2,600 m, *Steyermark 42770* (F, US). JAMAICA. Bull Head Mountain, *Hitchcock 9532* (US). MEXICO. CHIAPAS: Municipio de Jitotol, 5 km SE of Jitotol along road to Bochil, *Breedlove & Davidse 55114* (MO). VERACRUZ: San Miguel Jalapa, 6,500 ft., *Balls 4690* (US). VENEZUELA. FALCON: Paraguaná, Cerro Santa Ana, arriba de Santa Ana, 600 m, *Wingfield 7124* (VEN); Cerro Santa Ana, arriba de Santa María, 1,200 m, *Wingfield 6844* (MO).

**12b. Panicum dichotomum** var. **tenue** (Muhlenb.) Zuloaga & Morrone, comb. nov. *P. tenue* Muhlenb., Descr. Gram. 118. 1817. *Dichanthelium dichotomum* (L.) Gould var. *tenue* (Muhlenb.) Gould & C.A. Clark, Ann. Missouri Bot. Gard. 65: 1119. 1978. TYPE: *Muhlenberg Herb. 192* (lectotype PH-M not seen; fragment and photo of lectotype, US not seen).

*Panicum unciphyllum* Trin., Gram. Panic. 242. 1826. *Panicum acuminatum* Sw. var. *unciphyllum* (Trin.) Lelong, Brittonia 36: 269. 1984. *Dichanthelium ensifolium* (Elliott) Gould var. *unciphyllum* (Trin.) Hansen & Wunderlin, Ann. Missouri Bot. Gard. 75: 1647. 1988. *Dichanthelium dichotomum* (L.) Gould var. *unciphyllum* (Trin.) Davidse, Novon 2: 104. 1992. TYPE: North America: without locality, *Trattinick s.n.* (lectotype, LE not seen).

*Panicum albomarginatum* Nash, Bull. Torrey Bot. Club 24: 40. 1897. TYPE: United States. Florida: Lake County, June 1894, *Nash 925* (holotype, US 208344).

*Distribution and ecology:* eastern United States, Texas, Mexico, Belize, and the West Indies, in moist white-sand savannas, moist sandy woods, and marshy areas.

*Selected specimens cited.* BELIZE. EL CAYO: Mountain Pine Ridge, 550–700 m, *Davidse & Brant 33037* (MO). CUBA. ISLA DE LA JUVENTUD: Howard Estate, along Río Callejón, *Killip 44805* (US). PINAR DEL RIO: Arroyo Mántua, savannas, *Ekman 10994* (US); S of Guane, Sabana de San Julián, *León & Roca 7009* (US). MEXICO. CHIAPAS: Mun. La Trinitaria, montane rainforest at Lagos de Colores, Lagos de Montebello National Park, *Breedlove & Davidse 55038* (MO).

**13. Panicum divergens** HBK, Nov. Gen. & Sp. 1: 102. 1816. TYPE: Ecuador. Pichincha: Sangolquí, *Humboldt & Bonpland s.n.* (holotype, P; fragment, US 80645). Figures 24E, F, 27.

*Panicum commutatum* Schultes, Mantissa 2: 242. 1824. *Dichanthelium commutatum* (Schultes) Gould, Brittonia 26: 59. 1974. *Panicum nervosum* Muhlenb. ex Elliott, Sketch Bot. S. Carolina 1: 122. 1816, non Lam., 1797. *Panicum polyneuron* Steudel, Syn. Pl. Glumac. 1: 91. 1854. TYPE: United States. "Car. et Geor.," *Elliott Herb. s.n.* (lectotype, CHARL not seen; photo and fragment, US 80874).

*Panicum leiophyllum* Fourn., Mexic. Pl. 2: 20. 1886, non Nees, 1829. TYPE: Mexico. Veracruz: "in valle Cordobensi," Jan., *Bourgeau s.n.* (holotype, P).

*Panicum albomaculatum* Scribner, U.S.D.A. Div. Agrost. Cir. 19: 2. 1900. *Dichanthelium albomaculatum* (Scribner) Gould, Brittonia 32: 357. 1980. TYPE: Mexico. Michoacán: Patzcuaro, 10 Nov. 1892, *Pringle 5203* (holotype, US 743918).

*Panicum joorii* Vasey, U.S.D.A. Div. Agrost. Bull. 8: 31. 1889. *Panicum commutatum* Schultes var. *joorii* (Vasey) Fernald, Rhodora 39: 388. 1937. TYPE: United States. Louisiana: near Baton Rouge, 1 Oct. 1885, *Joor 39* (holotype, US 2808925).

*Panicum alsophilum* Swallen, Contr. U.S. Natl. Herb. 29: 422. 1950. TYPE: Guatemala. Jalapa: collected in oak woods around the top of Cerro Alcoba, just

E of Jalapa, 1,300–1,700 m, 2 Dec. 1939, *Steyermark 32513* (holotype, F; isotype, US 2236475).

*Panicum hintoni* Swallen, Contr. U.S. Natl. Herb. 29: 419. 1950. TYPE: Mexico. México: collected at Bejucos, Temascaltepec, 610 m, 8 Nov. 1932, *Hinton 2527* (holotype, US 1867697; isotype, US 1865776).

Short-rhizomatous perennial without basal rosettes of broader leaves, or rosettes occasionally present. *Culms* geniculate, decumbent and branching at the lower nodes to erect, freely branching at the middle and upper nodes, (15–)40–120 cm tall, internodes hollow, terete, short-pilose or glabrous, nodes dark, pilose. *Sheaths* striate, short papillose-pilose with caducous hairs or glabrous, one margin long-ciliate, the other glabrous. *Ligules* short-membranous at base and short- to long-ciliate at the apex, 0.2–0.4(–1) mm long; collar densely pilose. *Blades* lanceolate, 4–10(–16) cm long, 0.7–1.2(–1.7) cm wide, flat, clasping, asymmetric and cordate or subcordate at base, the apex attenuate, densely papillose-pilose with caducous hairs or glabrous, densely pilose toward the base on the adaxial surface, the margins ciliate toward the base, otherwise scabrous. *Inflorescences* terminal, exserted, peduncle glabrous, 20–30 cm long; *panicles* lax, diffuse, (3–)10–22 cm long, 6–10 cm wide; *main axis* flexuous, greenish to purplish, glabrous or short-hispid, glandular or eglandular, the pulvini brownish or purplish, glabrous, first-order branches alternate or subopposite, divergent, the axis of the branches and pedicels smooth, flexuous, scaberulous, glandular or eglandular. Axillary panicles present or absent, similar to the terminal one. *Spikelets* solitary, narrowly ellipsoid to obovoid, (2.1–)2.3–3.2 mm long, 1.2–1.3 mm wide, planoconvex, greenish to purplish, shortly and sparsely hispid. *Lower glume* 0.5–1.5 mm long, ¼ to less than ½ the length of the spikelet, ovate, 1-nerved, separated from the upper glume by a short internode. *Upper glume* covering the upper anthecium or not, acute, 7–9-nerved, the nerves anastomosing toward the apex. *Lower lemma* acute, 7–9-nerved, the nerves anastomosing toward the apex. *Lower palea* lanceolate, 1.3–2 mm long, 0.4 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid or obovoid, 2.3–3 mm long, 1–1.1 mm wide, smooth, whitish, indurate, shiny, papillose, the apex of the lemma shortly apiculate and with unicellular macrohairs. *Caryopsis* obovoid, 1.3 mm long, 1 mm wide; hilum punctiform, embryo less than ½ the length of the caryopsis.

*Distribution and ecology:* eastern United States to Mexico and Guatemala and the West Indies (see discussion of the possible presence in Ecuador); it grows at the margins of pine or oak woods or in open field borders, to 2,700 m.

*Selected specimens cited.* CUBA. HABANA: clearing in swampy wood, W of Batabanó, *León 14201* (US). ORIENTE: Guantánamo, Monte Libanon, *Ekman 10297* (US). SANTA CLARA: banks of a canal, S border of Ciénaga de Zapata, *Roig 2205* (US). GUATEMALA. CHIMALTENANGO: Chichavac, *Skutch 524* (US). HAITI. Massif du Nord, *Ekman 6189* (US). HONDURAS. OCOTEPEQUE: Aldea de Belén Gualcho y alrededores; 40 km al E de Nueva Ocotepeque, *Nelson et al. 3800* (UNAH). MEXICO. CHIAPAS: Mun. Jitotol, near Colonia El Laurel, ca. 5 km N of Jitotol, *Davidse et al. 29630* (MO). JALISCO: Zapotlán, *Hitchcock s.n., Amer. Gr. Herb. 193* (MO, P). MICHOACAN: Uruapán, *Hitchcock s.n., Amer. Gr. Herb. 226* (F, MO, P). MORELOS: Huitzilac, *Lyonnet 623* (MO). NAYARIT: 8 mi. W of Tepic, *McVaugh 18881* (US). NUEVO LEON: 12 mi. S of Monterrey, *Mueller 414* (US). VERACRUZ: Jalapa, *Hitchcock s.n., Amer. Gr. Hb. 225* (MO).

The type locality of *P. divergens* is, according to Humboldt, Bonpland & Kunth, Sangolguí in Pichincha province, Ecuador. This is probably a label error since Humboldt also made collections in Mexico, where this species is commonly found. Another possible explanation is that the species has, as in the case of *P. umbonulatum*, a disjunct distribution.

**14. Panicum ensifolium** Baldwin ex Elliott, Sketch Bot. S. Carolina 1: 126. 1816. *Panicum nitidum* Lam. var. *ensifolium* (Elliott) Vasey, U.S.D.A. Div. Agrost. Bull. 8: 29. 1889. *Dichanthelium ensifolium* (Elliott) Gould, Brittonia 26: 59. 1974. *Dichanthelium dichotomum* (L.) Gould var. *ensifolium* (Elliott) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1119. 1978. TYPE: United States. Georgia: without locality, *Baldwin s.n.* (holotype, CHARL not seen; fragment, US). Figure 27.

*Panicum chamaelonche* Trin., Gram. Panic. 242. 1826. TYPE: "V. Spp. Am. bor. (*Trattinick ex coll. Enslini*)," (holotype, LE not seen).

Densely tufted perennial. *Culms* erect, 8–30 cm tall, frequently unbranched above the base; internodes terete, greenish to purplish, pilose, nodes shortly pilose. *Sheaths* striate, greenish or purplish, glabrous, the margins membranous, ciliate or only pilose near the ligule. *Ligules* 0.4 mm long, membranous-ciliate, the membranous portion reduced. *Blades* linear, 2–6.5 cm long, 0.1–0.3 cm wide, rounded at base, flat to slightly involute, greenish or purplish, sparsely pilose on the adaxial surface or glabrous, the margins scabrous. *Inflorescences* terminal and axillary from the uppermost nodes,

short-exserted, peduncles up to 5 cm long, cylindric, glabrous; panicles 1–4.5 cm long, main axis purplish, flexuous, glandular or eglandular, scabrous or glabrous; pulvini glabrous, the branches alternate, divergent, axis of the branches and pedicels flexuous, scabrous or glabrous, greenish or purplish, glandular or eglandular. Axillary panicles numerous, similar to the terminal one. *Spikelets* obovoid to ellipsoid, 1–1.4 mm long, 0.5–0.6 mm wide, greenish to purplish, shortly hispid or glabrous. *Lower glume* 0.4 mm long, ⅓ the length of the spikelet, truncate to acute, nerveless, hyaline. *Upper glume* obtuse, shorter than the lower lemma and not covering the upper anthecium, 5–7-nerved. *Lower lemma* as long as the spikelet, 5-nerved. *Lower palea* lanceolate, 0.5–0.7 mm long, 0.3 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 0.9–1.2 mm long, 0.4–0.6 mm wide, indurate, smooth and shining, pale, papillose; lemma 5-nerved. *Caryopsis* obovoid, black, 0.6–0.8 mm long, 0.5 mm wide; hilum punctiform, embryo ⅓–⅖ the length of the caryopsis.

*Distribution and ecology:* United States, Belize, and Cuba, in pine white-sand savannas, 0–100 m.

*Selected specimens cited.* BELIZE. 3 mi. W of Boomtown, *O'Neill 8500* (MO, US); pine ridge N of aviation field, *Bartlett 11236* (MO, US). CUBA. ISLA DE LA JUVENTUD: vicinity of Los Indios, *Britton et al. 14218* (US), *14221* (MO, US). PINAR DEL RIO: km 13 on La Coloma road, *León & Alain 19474* (US); Damují at Rincón del Prado, *Ekman 11047* (US); Laguna Santa Bárbara, *Ekman 11465* (US).

*Panicum ensifolium* has many fascicled culms branching from the base, spikelets 1–1.4 mm long, and a black caryopsis.

**15. Panicum hebotes** Trin., Mém. Acad. Imp. St.-Pétersb., Ser. 6, Sci. Math 1: 301. 1834. *Panicum hebotes* Trin. var. *genuinum* Doell in C. Martius, Fl. Bras. 2(2): 252. 1877, nom. illeg. TYPE: Brazil. "V. sp. Bras" (holotype, LE; fragment, US 974693). Figures 8, 27, 33.

*Panicum mirandum* Luces, J. Wash. Acad. Sci. 32: 163, fig. 8. 1942. TYPE: Venezuela. Miranda: Guinand Estate (Cárdenas), Siquire Valley, 500–1,000 m, 19–24 Mar. 1913, *Pittier 6483* (holotype, US 602176; isotype, NY).

*Panicum infuscum* Swallen, Phytologia 14: 82. 1966. TYPE: Brazil. Rio de Janeiro: Tijuca, 700 m, 28 Apr. 1930, *Chase 12145* (holotype, US 1448475).

*Panicum subtiliracemosum* Renvoize, Kew Bull. 42: 922. 1987. *P. subtipaniculatum* Renvoize, Hatschbach's Paraná Grasses: 39. 1988, error for *P. subtiliracemosum*. TYPE: Brazil. Paraná: Cachoeira dos Turcos, *Hatschbach 46020* (holotype, MBM; isotype, K).

Plants perennial. *Culms* decumbent, rooting and branching at the lower nodes, then becoming erect, 30–90 cm tall, leaning on vegetation, internodes 3.5–15 cm long, hispid, hollow, nodes compressed, pilose, brownish. *Sheaths* 2.5–7.5 cm long, shorter than the internodes, hispid, one margin ciliate, the other membranous. *Ligules* 0.3 mm long, membranous and laciniate at the apex, collar hispid. *Blades* lanceolate, 4.5–15 cm long, 0.7–2.3 cm wide, flat, hispid or with the adaxial surface glabrous, narrowed at the base, occasionally cordate, the apex attenuate, the margins scabrous. *Inflorescences* terminal, usually long-exserted, peduncle 12–32 cm long, hirsute; panicles lax, diffuse, 7–22 cm long, 4.5–11 cm wide; *main axis* flexuous, hispid, eglandular, first-order branches alternate to subopposite, second- and third-order branches glabrous or sparsely pilose, eglandular; pedicels scabrous, terete. *Spikelets* ellipsoid, 1.5–1.9 mm long, 0.6–0.9 mm wide, scaberulous toward the distal portion of the upper glume and lower lemma, otherwise puberulous or glabrous, greenish, the upper glume and lower lemma subequal with manifest nerves; internodes inconspicuous between the lower glume and upper anthecium. *Lower glume* 0.7–1.5 mm long, ovate, acute to obtuse, 3–7-nerved, glabrous, not embracing the upper glume, dimorphic, some small, ⅖ the length of the spikelet, 1–3-nerved, other longer, ¾ the length of the spikelet, 7-nerved. *Upper glume* 1.4–1.7 mm long, 9-nerved, not covering the apex of the upper anthecium. *Lower lemma* glumiform, 9-nerved. *Lower palea* lanceolate, 0.7–1.2 mm long, 0.3 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 1.3–1.7 mm long, 0.7–0.8 mm wide, indurate, smooth, shiny, pale to brownish or black at maturity, puberulous at the apex, papillose, shortly apiculate, lodicules 0.2 mm long, stamens 3, the anthers 0.7 mm long; stigma whitish. *Caryopsis* ellipsoid, 1 mm long, 0.6 mm wide, brownish, hilum punctiform, embryo less than ⅓ the length of the caryopsis.

*Distribution and ecology:* forest edges in Venezuela, Ecuador, Bolivia, and Brazil, from 500 to 1,800 m.

*Additional specimens examined.* BOLIVIA. LA PAZ: Yungas, *Bang s.n.*, 1890 (G, K, MO, NY, US 823922, W). BRAZIL. CEARA: Baturité, *Eugenio 285* (RB, US), *2649* (RB). ESPIRITO SANTO: Santa Teresa, Reserva Biológica de Nova Lombardía, Picada da Cachoeira, *Zuloaga et al. 2423, 2425* (RB, SI, US). MINAS GERAIS: Itacolumí, E of Ouro Preto, 1,300 m, *Chase 9408* (MO, NY, US);

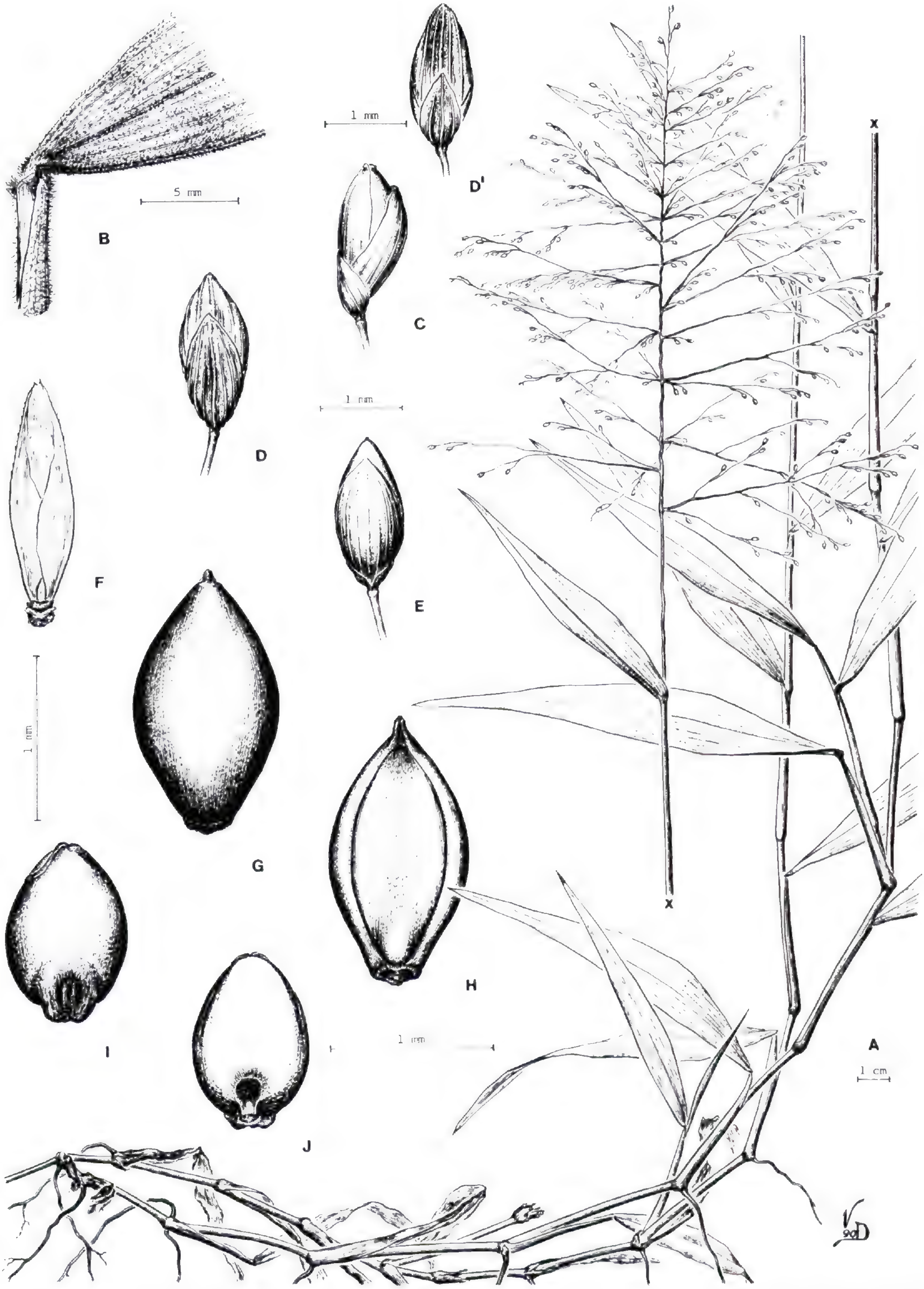


FIGURE 33. *Panicum hebotes.*—A. Habit, with panicle included.—B. Detail of ligule and lower portion of the blade.—C. Spikelet, lateral view.—D. Spikelet, lower glume view.—E. Spikelet, upper glume view.—F. Lower palea.—G. Upper anthecium, lemma view.—H. Upper anthecium, palea view.—I. Caryopsis, embryo view.—J. Caryopsis, hilum view. (A, based on *Brade 20119*, B–J, based on *Chase 9640*.)

Serra do Caparaó, *Chase 9640* (F, MO, NY, US). PARANA: Marumbí, *Dombrowski 3943* (K, PKDC). RIO DE JANEIRO: Tijuca, 1,000 m, *Chase 12162, 12165* (US); Corcovado, *Chase 8182, 9745* (MO, NY, US); Floresta sob regime de Preservaçào Permanente do IBDF, entre Vale dos Princesas y Rocío, *Zuloaga et al. 2390** (MO, RB, SI, US); Parque Nac. Itatiaia, Picada Três Picos, *Zuloaga et al. 2373** (RB, SI, US); S of Petrópolis, 530 m, *Davidse et al. 11411* (MO, SI); vicinity of Rio de Janeiro, Pico da Tijuca, *Chase 8484* (MO, NY, US); Vista Chinesa, *Brade 20119* (US). RIO GRANDE DO SUL: without locality, *Orth 1938* (US). SANTA CATARINA: Três Barras, Garuva, *Reitz & Klein 5561* (US). SÃO PAULO: 38 km SW of Jacupiranga along Hwy. 116 to Curitiba, *Davidse et al. 10949* (MO, SI, SP); Cananeia Island, 1 km NE of city along W shore of island, *Clayton & Eiten 4741* (K, NY, SP, UB, US); Parque do Estado, *Clayton & Eiten 4190* (K, NY, SP); 19 km SW of Juquitiba, along Hwy. 116 to Curitiba, *Davidse et al. 10933* (SP). COLOMBIA. NARIÑO: Mun. Ricaurte, vicinity of Ricaurte, along Río Imbí, ca. 2–3 km above Ecopetrol Campamento Palmar, 3 km NW of Ricaurte, along trail to Ramos, 1,150 m, *Croat 71502* (MO). ECUADOR. TUNGURAHUA: valley of Pastaza River, between Baños and Cachurco, 1,300–1,800 m, *Hitchcock 21862* (NY, US). VENEZUELA. ARAGUA: Alto de Choroní, Parque Nacional Henry Pittier, carretera de Maracay a Choroní, 1,560 m, *Zuloaga et al. 4534** (MO, SI, VEN). BOLIVAR: E of Cerro El Picacho, N of Las Nieves and Las Chicharras, 45 km N of Tumeremo, vicinity of Deborah, Altiplanicie de Nuria, 600–650 m, *Steyermark 89073* (NY, US, W). DISTRITO FEDERAL: El Junquito, en la sombra de la selva, 1,900 m, *Shnee 484* (MY). SUCRE: Distrito Nariño and Distrito Arismendi, Península de Paria, trail between crossing of Río Tacarigua to summit of slopes E of Cerro Humo, descending to Las Melenas, *Steyermark et al. 121762* (NY, US). YARACUY: Distrito Nirguá, 5 km N of Nirguá by road, 10°12′N, 68°34′W, 1,200 m, *Davidse et al. 20904* (MO, VEN).

The type material of *P. hebotes* and *P. mirandum*, together with the other specimens examined, indicate that there are no differences between these taxa. Geminate spikelets, characteristic of Venezuelan specimens, are also occasionally present in other specimens from Bolivia and Brazil.

*Panicum subtiliracemosum* is also considered to be a synonym of *P. hebotes*. The Brazilian specimens cited by Renvoize (1987) under *P. subtiliracemosum* include *Dombrowski 2899* and *Hatschbach 38052*, which are included under *P. schawckeanum* Mez, a species of section *Parvifolia* (A. Hitchc. & Chase) Pilger. *Hatschbach et al. 13731* (K), considered by Renvoize as an intermediate specimen between *P. stigmosum* and *P. subtiliracemosum*, is indeed *P. surrectum*. *Chase 9408* has peculiar cordate blades; however, it shares similar spikelets, dark anthecia, and asymmetrical blades with other specimens of *P. hebotes*.

Anatomically, *P. hebotes* has a distinctive keel incorporating three vascular bundles (Fig. 8A, C). Adaxial ribs and wide, shallow furrows are present, and the mesophyll is diffuse but nevertheless of the semiradiate type (Fig. 8B, D). The three-celled microhairs (Fig. 9B, D) are unique to this species in the section and occur on all three specimens examined anatomically.

**16. Panicum heliophilum** Chase ex Zuloaga & Morrone, Ann. Missouri Bot. Gard. 78: 152. 1991. TYPE: Brazil. Minas Gerais: Chapéu do Sol, Serra do Cipó, 110 km NE of Belo Horizonte, 900 m, 28 Mar.–1 Apr. 1925, *Chase 9147* (holotype, US; isotypes, F, GH, MO, NY). Figure 27.

Short-rhizomatous perennial. *Culms* 50–70(–100) cm tall, tangled, leaning on vegetation, the basal portion decumbent and geniculate, the upper portion erect, freely branching; internodes cylindric, pilose, solid toward the base, otherwise hollow; nodes many, villous. *Sheaths* striate, 0.5–4 cm long, strongly distichous, hispid with short hairs, the margins long-ciliate; auricles small, pilose; collar brownish or purplish, covered with short whitish hairs. *Ligule* a ciliate membrane, 0.2–0.7 mm long, the cilia 0.1–0.6 mm long. *Blades* linear-lanceolate, 4–5(–12) cm long, 0.3(–1) cm wide, flat or folded, subcordate, densely hirsute on both surfaces, the margins cartilaginous, scabrous and short-ciliate. Primary *inflorescences* terminal, exserted, peduncles hispid, to 8 cm long; *panicles* lax, diffuse, 4–16 cm long, 3–13 cm wide; *main axis* flexuous, sparsely hirsute, eglandular, the pulvini brownish, hispid; first-order branches opposite or alternate, the lower ones whorled or not, diverging from the axis; axis of the branches short-hirsute or glabrous; pedicels smooth, glabrous, 2–13 mm long. Axillary panicles similar to the terminal one, smaller. *Spikelets* solitary, ellipsoid, 2.6–3.1 mm long, 1–1.1 mm wide, hirsute, greenish, without a stipe between the lower and upper glume. *Lower glume* 2–2.7 mm long, ¾ the length of the spikelet, acuminate, not embracing the upper glume at its base, 3-nerved, the nerves anastomosing toward the distal portion. *Upper glume and lower lemma* subequal, 7-nerved. *Lower palea* elliptic, 2 mm long, 0.3 mm wide, hyaline; lower flower absent. *Upper anthecium* narrowly ellipsoid, 2.4–2.7 mm long, 0.8–0.9 mm wide, stramineous, brownish at maturity, papillose, with simple papillae evenly distributed over the lemma and palea, densely pilose, with appressed, long hairs toward the apex of the lemma and palea; lemma 5–7-nerved, rachilla prolonged or not into a short mucro above the upper anthecium; lodicules ca. 0.6 mm long; stamens 3, the anthers ca. 1.3 mm long, purplish. *Caryopsis* ellipsoid, 1.4 mm long,

0.8 mm wide, brownish; hilum oblong, embryo ⅓ the length of the caryopsis.

*Distribution and ecology:* campos rupestres in Minas Gerais, Brazil, in sandy soils between 900 and 1,400 m.

*Additional specimens examined.* BRAZIL. MINAS GERAIS: Diamantina, summit of Serra de San Antonio, 1,400 m, *Chase 10354* (US); Mun. Jaboticatubas, Lagoa Santa a Conceição do Mato Dentro, *Sendulsky & Burman 1920* (SI, SP); km 114 ao largo da rodovía Lagoa Santa–Conceição do Mato Dentro, 1,160 m, *Sendulsky 1609* (SP); Saramenha, *Gomes 3955* (US); Serra de Santo Antonio, 2–5 km ao E de Diamantina, 1,050–1,100 m, *Burman & Sendulsky 696, 697, 709* (SI, SP); Serra do Cipó, ao longo da rodovia Lagoa Santa–Conceição, *Sendulsky 446* (SP); Serra do Cipó, *Burman 525* (SP), *Burman 485* (SP); Serra de Itatiaia e Serra de Lavras Novas, *Burman 384* (SP); Serra de Ouro Branco, *Castellanos 25628* (HB); Serra de Cipó, Mun. Jaboticatubas, km 116 ao longo da rodovia Lagoa Santa, 6 June 1970, *Joly et al. 100* (SP); Metallúrgica, Serra de Ouro Branco, 1,250–1,600 m, *Chase 10289* (MO).

Affinities of *P. adenorhachis* are discussed in Zuloaga & Morrone (1991).

**17. Panicum itatiaiae** Swallen, Phytologia 14: 82. 1966. TYPE: Brazil. Rio de Janeiro: Parque Nacional Itatiaia, Picada Macieiras, 1,700–1,800 m, 18 Jan. 1925, *Chase 8327* (holotype, US 1255836; isotypes, F 561591, GH, NY, US 1258426). Figures 28, 36.

Perennial. *Culms* geniculate, decumbent and rooting at the lower nodes, ascendent and branching at the upper nodes, more than 1 m tall, internodes 3–14 cm long, terete, rigid, hollow, glabrous, nodes purplish, glabrous. *Sheaths* 3–8 cm long, usually shorter than the internodes, glabrous with only one margin ciliate. *Ligules* 0.3–0.4 mm long, membranous at the base and short-ciliate or laciniate at the distal portion; collar purplish, short-pilose. *Blades* lanceolate or ovate-lanceolate, 10–12 cm long, 1–1.4 cm wide, flat, subcordate, glabrous, with long hairs close to the ligular region, the midnerve manifest, the margins ciliate and scabrous. *Inflorescences* terminal, exserted, peduncles cylindric, to 40 cm long, glabrous; *panicles* lax, diffuse, 13–18 cm long, 10–20 cm wide; *main axis* flexuous, smooth, glabrous, pulvini brownish, glabrous, first-order branches divergent, alternate or opposite, the axis of the branches triquetrous, purplish, scabrous; pedicels smooth, glabrous, purplish, 3–8 mm long. *Spikelets* solitary, narrowly ellipsoid, 4.6–5 mm long, 1.6–1.7 mm wide, glabrous, greenish, tinged with purple, the upper glume and lower lemma subequal. *Lower glume* 2.6–3.2 mm long, ½ or more the length of the spikelet, acuminate, 5-nerved, glabrous, separated from the upper glume by a short internode. *Upper glume* 4–4.3 mm long, usually not covering the apex of the upper anthecium, obtuse, (11–)13-nerved, the nerves anastomosing toward the apex, the outer surface scaberulous, herbaceous. *Lower lemma* 4.3–4.6 mm long, 13-nerved, the nerves anastomosing toward the apex, acute, scaberulous. *Lower palea* ovate-lanceolate, 4–4.1 mm long, 1–1.1 mm wide, membranous, the margins short-ciliate; lower flower male, the stamens 3, the anthers 2.2 mm long. *Upper anthecium* lanceolate, 4–4.2 mm long, 1.3–1.6 mm wide, apiculate, scabrous and sparsely pilose toward the apex, otherwise glabrous, papillose, with small simple papillae regularly distributed over its entire surface; lemma 7-nerved, the palea scabrous at its apex. *Caryopsis* obovoid, 2.5 mm long, 1.5 mm wide, brownish; hilum punctiform, embryo ⅛ the length of the caryopsis.

*Distribution and ecology:* known only from the type collection made in the Sierra de Itatiaia, in Rio de Janeiro, Brazil, in forests at 1,700–1,800 m; collected under bamboo, with the base long-decumbent.

When describing this species, Swallen indicated that spikelets were 4–4.5 mm long, but none of the types examined had any spikelets within this range.

**18. Panicum laxiflorum** Lam., Encycl. 4: 748. 1798. *Dichanthelium laxiflorum* (Lam.) Gould, Brittonia 26: 60. 1974. *Panicum dichotomum* L. var. *laxiflorum* (Lam.) Beal, Grasses N. Amer. 2: 139. 1896. TYPE: United States. Without locality and collector (holotype, P-LAM; fragment and photo, US 2808927). Figure 27.

*Panicum xalapense* HBK, Nov. Gen. & Sp. 1: 103. 1816. TYPE: Mexico. Veracruz: near Jalapa, *Humboldt & Bonpland s.n.* (holotype, P).

*Panicum ruprechtii* Fourn., Mexic. Pl. 2: 21. 1886, non Fenzl, 1854. TYPE: Mexico. Veracruz: Jalapa, *Galeotti 5733* (holotype, BR not seen).

*Panicum caricifolium* Scribner ex Ashe, J. Elisha Mitchell Sci. Soc. 15: 57. 1898. TYPE: United States. Maryland: Great Falls, *Kearney Jr.*, 23 May 1897 (isotype, NY).

*Panicum pyriforme* Nash, Bull. Torrey Bot. Club 26: 579. 1899. TYPE: United States. Florida: Lake County, Eustis, 12–31 Mar. 1894, *Nash 239* (holotype, NY; isotype, US 221672).

*Panicum xalapense* HBK var. *strictirameum* A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 161. 1910. TYPE: United States. Mississippi: in small close bunches, Jackson, 28 Apr. 1906, *Hitchcock 1311* (holotype, US 558449).

Perennial. *Culms* densely caespitose, fasciculate, internodes very short at base of the plants, culms decumbent, profusely branching at the lower nodes, then erect, few-noded, 5–30(–40) cm tall; internodes terete, glabrous, hollow; nodes brownish, densely pilose with long whitish hairs. *Sheaths* striate, hirsute with rigid papillose-pilose hairs, the margins membranous. *Ligules* membranous-ciliate, 0.3–0.9 mm long, the pseudoligule absent; collar pale, densely pilose. *Blades* lanceolate, 3–15 cm long, 0.2–0.8(–1) cm wide, flat, narrowed at base, acuminate, the margins long-ciliate, papillose-pilose on both surfaces or only on the upper portion of the adaxial surface or glabrous, the midnerve not manifest. Terminal and axillary *inflorescences* similar, short-exserted or included on the upper leaves; peduncle terete, hirsute or glabrous, to 15 cm long; *panicles* lax, 2–9 cm long, 2–7 cm wide; *main axis* flexuous, densely hirsute or glabrous, glandular or eglandular; pulvini long-pilose, first-order branches alternate, divergent, the axis of the branches smooth, sparsely hirsute or glabrous, glandular or eglandular; pedicels long, sparsely hispid. *Spikelets* solitary, plano-convex, ellipsoid to more commonly obovoid, 2–2.7 mm long, 1–1.4 mm wide, short-hirsute, greenish, upper glume and lower lemma subequal. *Lower glume* ovate-acuminate, 0.8–1.3 mm long, ⅓–½ the length of the spikelet, 1–3-nerved. *Upper glume* acute, 9-nerved, covering the apex of the upper anthecium or not. *Lower lemma* glumiform, 9-nerved. *Lower palea* elliptical, 1–1.4 mm long, 0.5–0.7 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* broadly ellipsoid, 1.8–2.3 mm long, 1–1.4 mm wide, indurate, smooth, shiny, papillose, lemma apiculate, the apex greenish. *Caryopsis* broadly obovoid, brownish, 1.3 mm long, 1.2 mm wide; hilum punctiform, embryo a little less than ½ the length of the caryopsis.

*Distribution and ecology:* eastern United States and Mexico to Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, and the West Indies, in Cuba, the Dominican Republic, and Haiti. Inhabits moist banks and edge of pine and oak woods or mixed hardwood forest, between 700 and 2,700 m.

*Selected specimens cited.* COSTA RICA. CARTAGO: 3 km up mountain from Tejar, Pan-American Hwy., *Taylor & Taylor 11842* (MO, US). SAN JOSE: 5.5 km by road NW of San Pablo, *Pohl & Pinette 13123* (MO). CUBA. ORIENTE: Sierra Maestra, La Gran Piedra above Daiquirí, *Ekman 1604* (G, US). PINAR DEL RIO: Consolación del Sur, pineland hills at Juan Moreno, *Ekman 10860* (G, NY, US). DOMINICAN REPUBLIC. AZUA: Sierra de Ocoa, San José de Ocoa, *Ekman 11855* (US). LA VEGA: 5 km N of Tireo, NE of Constanza, *Gould & Jiménez 14112* (MO). SAN JUAN: Sabana Nueva, 6,200 ft., N of Río Arriba, *Howard & Howard 9079* (US). SANTIAGO: Jiromé, 700 m, *Valeur 293* (MO, US). GUATEMALA. ALTA VERAPAZ: cut-over steep slopes 3 mi. E of Tactic on Route 7E toward Tamahu, *Wilbur 14916* (MO). BAJA VERAPAZ: 6 km N of El Chol, *Harmon & Dwyer 3168* (MO). HAITI. M. des Commissaires, *Holdridge 1729* (MO); vicinity of St. Louis du Nord, mountain SW of city, *Leonard & Leonard 14503* (US). HONDURAS. CHOLUTECA: San Marcos de Colón, *Izaguirre 53* (MO). INTIBUCA: Cerro San Cristóbal, La Esperanza, *Ordoñez 84* (MO). FRANCISCO MORAZAN: Parque La Tigra, *Cruz 70* (MO). OCOTEPEQUE: Belén Gualcho, 4 km from town on road from Corquín, *Blackmore & Chorley 3838* (MO). OLANCHO: Montana Los Zapotes, 10 km NO de Campamento, *Soto 44* (MO). MEXICO. Chinantlá, *Liebmann 328* (MO). CHIAPAS: Mun. Tenejapa, in the Paraje Kurus Ch'en, *Breedlove 28188* (MO); 65 km N of the junction Mex 190 and 195 on Mex 195, *Brunken & Perino 336* (MO); Mun. Jitotol, near Colonia El Laurel, ca. 5 km N of Jitotol, *Davidse et al. 29621* (MO). HIDALGO: along Hwy. 105 between Pachuca and Tampico, along road to San Cristóbal which leaves main highway 100.8 mi. NE of Pachuca vicinity of turnoff, 1.5 km from San Cristóbal, *Croat & Hannon 65910* (MO). OAXACA: 3.5 km al S de San Andrés Yaa, en la desviación a Oaxaca, *Torres 2020* (MO). PUEBLA: 0.8 mi. S of Zacapoaxtla on road from Zaragoza, *Brunken & Perino 265* (MO); Trinidad Iron Works, *Pringle 13250* (MO). QUERETARO: off road from Jalpán to Xilitla, 5.8 mi. W of San Luis Potosí state line, *Thomas 2794* (MO). VERACRUZ: 3 km NE of Jilotepec on road to Naolinco, *Nee & Taylor 26237* (MO); Córdova, *Bourgeau 2162* (MO). NICARAGUA. ESTELI: lado S del Cerro Tomabú, por el Valle Las Cuevas, *Moreno 18455* (MO); N slope of Cerro El Fraile, ca. 13°25'N, 86°16'W, *Stevens & Montiel 18103* (MO). JINOTEGA: along Hwy. 3 ca. 1.9 km NW of Aranjuez road entrance, *Stevens 5578* (MO). MADRIZ: San Jose de Cusmapa, 1 km al E del Cerro de Buenavista, *Moreno 14360* (MO). MATAGALPA: El Ocotal, 4 km al S de Matagalpa, *Moreno 17656, 17694* (MO).

**19. Panicum pedicellatum** Vasey, U.S.D.A. Div. Bot. Bull. 8: 28. 1889. *Dichanthelium pedicellatum* (Vasey) Gould, Brittonia 26: 60. 1974. TYPE: United States. Texas: Kimble Co., rocky woods, June 1885, *Reverchon 1620* (holotype, US 2383607; isotypes, MO, NY). Figure 27.

*Panicum transiens* Swallen, J. Wash. Acad. Sci. 21: 436. 1931. TYPE: Mexico. Tamaulipas: Sierra de San Carlos, Mesa de Tierra, vicinity of San José, 1,000 m, 19 July 1930, *Bartlett 10454* (holotype, US 1501526).

Tufted perennial. *Culms* erect to ascending, 15–30(–60) cm tall, simple at the base, freely branching at the middle and upper nodes; internodes cylindric, hollow, shortly pilose with tuberculate hairs, the margins membranous, glabrous or shortly pilose. *Ligules* membranous-ciliate, 0.3–0.6 mm long; collar shortly pilose. *Blades* lanceolate, 5–8.5 cm long, 0.2–0.8(–1.3) cm wide, flat, subcordate, the

lower margins long-ciliate, the adaxial surface pilose with appressed, whitish hairs, the abaxial surface shortly pilose or glabrous. *Inflorescence* terminal and axillary from the uppermost nodes, short to long-exserted, peduncle cylindric, 5–20 cm long, shortly pilose; *panicles* few to multiflowered, 3–8(–10) cm long; *main axis* flexuous, shortly pilose, the pulvini shortly pilose, branches alternate, divergent, the axis of the branches pilose; pedicels paired, unequal, 2–12 mm long, triquetrous, pilose or scaberulous. *Spikelets* narrowly ellipsoid, 3.3–4.1 mm long, 1.3–1.5 mm wide, short-papillose-pilose, greenish to purplish. *Lower glume* ovate-acuminate, 1.8–2.2 mm long, ½ the length of the spikelet or less, 3–5-nerved, separated from the upper glume by a distinct internode, not embracing the upper glume. *Upper glume* obovate or ovate, 3.2 mm long, obtuse, not covering the apex of the upper anthecium, 9–11-nerved, the nerves anastomosing toward the apex. *Lower lemma* 9-nerved, pilose. *Lower palea* 1.2–1.9 mm long, 0.4 mm wide, lanceolate, hyaline, glabrous; lower flower absent. *Upper anthecium* narrowly ellipsoid, 3–3.5 mm long, 1.2 mm wide, indurate, smooth, shining, papillose and with prickle hairs at the apex. *Caryopsis* unknown.

*Distribution and ecology:* United States, in Texas, Mexico, and occasionally in Guatemala, growing in moist, shaded places, on rocky slopes, bordering rivers or in open pine or oak woods, to 2,500 m.

*Additional specimens examined.* GUATEMALA. EL PROGRESO: hills between Finca Piamonte and slopes SE of Finca Piamonte, *Steyermark 43463* (F). MEXICO. COAHUILA: middle and upper reaches of Cañón de la Hacienda, almost due S of Rancho Cerro de la Madera, N slope of Sierra de la Madera, 2,000–2,500 m, 27°03′N, 102°25′W, *Chiang et al. 9452* (MO), *Johnston et al. 10974* (MO). NUEVO LEON: Dulces Nombres, 1,310 m, *Meyer & Rogers 2663* (MO). UNITED STATES. TEXAS: Kerrville, *Heller 1736* (MO), 2,000 ft.; Comanche Springs, *Lindheimer 1265* (MO); along banks of Guadalupe River, near Kerrville, *Palmer 33820* (MO).

**20. Panicum penicillatum** Nees ex Trin., Gram. Panic. 196. 1826. TYPE: Brazil. Without locality, *Langsdorff s.n.* (holotype, LE not seen). Figures 25, 36.

*Panicum discolor* Trin. ex Nees, Agrost. Brasil.: 144. 1829, non Sprengel, 1807. TYPE: Brazil. Minas Gerais: "Habitat in fruticetis umbrosis prope Tejuco," *Langsdorff s.n.* (holotype, LE; fragment, US).

*Panicum phragmites* Nees, Agrost. Brasil.: 190. 1829. TYPE: Brazil. Without locality, *Sellow s.n.* (holotype, B; fragment, BAA, US; isotype, K).

Perennial. *Culms* decumbent, rooting and branching at the lower nodes, leaning on vegetation and scandent, reaching up to 10 m, internodes 8–18 cm long, solid on the lower portion, rigid, cylindric and pilose; nodes dark, thickened, densely pilose with long whitish hairs or glabrous. *Sheaths* 10–14 cm long, the lower ones shorter and the upper ones longer than the internodes, papillose-pilose with long tuberculate, caducous hairs or glabrous, one margin ciliate, the other membranous, auricles membranous. *Ligules* ca. 0.5 mm long, membranous, lacerate on the upper portion; collar brownish, shortly pilose or glabrous. *Blades* lanceolate, 18–32 cm long, 1.2–3.2 cm wide, flat, pseudopetiolate, the pseudopetiole brownish, puberulous; blades narrowed to subcordate, slightly asymmetrical, the apex long-attenuate, sparsely pilose or glabrous, the abaxial surface usually glaucous, the margins scabrous. *Inflorescences* terminal, exserted, peduncle cylindric, glabrous; *panicles* lax, diffuse, multiflowered, 30–45 cm long, 20–40 cm wide; *main axis* flexuous, scabrous or glabrous, the pulvini brownish, glabrous, first-order branches divergent, alternate or opposite, occasionally whorled toward the base, the axis of the branches scabrous; pedicels scabrous, triquetrous. *Spikelets* solitary, narrowly ellipsoid, 3–4.2 mm long, 1.1–1.4 mm wide, greenish to purplish, the upper glume and lower lemma subequal, acute, with strong nerves. *Lower glume* 2.8–3.6 mm long, as long as or a little shorter than the upper glume, 3–5-nerved, acuminate to subulate, pilose toward the apex, scabrous on the inner surface. *Upper glume* 3–4 mm long, acute, (7–)9–11-nerved, shortly pilose toward the apex, pilose on the inner surface. *Lower lemma* glumiform, 3–4.1 mm long, 9–11-nerved, pilose on the inner surface. *Lower palea* absent; lower flower absent. *Upper anthecium* narrowly ovoid, 3.2–3.7 mm long, 1–1.3 mm wide, stramineous, with simple papillae regularly distributed over its entire surface, lemma apiculate, the apex and upper margins pilose. *Caryopsis* narrowly ellipsoid, 2.2–2.4 mm long, 1.2 mm wide, brownish; hilum punctiform, embryo a little less than ½ the length of the caryopsis.

*Distribution and ecology:* Brazil, in the Distrito Federal and the states of Goiás, Minas Gerais, and Rio de Janeiro, in dense colonies at forest edges, where it grows leaning on vegetation, from 450 to 1,500 m.

*Additional specimens examined.* BRAZIL. DISTRITO FEDERAL: Bacia do Rio São Bartoloméu, Equipe IBGE 3572 (IBGE); próximo a Sobradinho, *Filgueiras 1964* (IBGE, MO). GOIAS: capoeira and gallery margin, ca. 12 km S de Corumbá de Goiás, 1,000 m, *Irwin et al. 10848* (MO, NY, US); Santo Antonio do Descoberto, fazenda de Agricultura Natural, 13 Dec. 1989, *Alvarenga & Oliveira 525* (IBGE, SI). MINAS GERAIS: Viçosa, *Chase 9465*,

(F, US), 640 m, between São Geraldo and Viçosa, *Chase 10200, 10217* (US), *Kuhlmann 1942* (IAN, RB), *Pires & Black 2844* (IAN, US); Fazenda do Aguada, Cabeçeira do Matto, 750 m, *Mexía 5368* (F, G, GH, K, NY, P, US); Serra do Cipó, 1,200 m, *Anderson et al. 36155* (F, K, MO, UB, US), 800 m, km 103, *Chase 9288* (F, MO, NY, US); Serra do Espinhaço, Serra do Itabirito, 50 km SE of Belo Horizonte, *Irwin et al. 19727* (MO, UB, US); Barbacena, Serra Mantiqueira, *Chase 8716* (F, GH, NY, US); Anna Florencia, E of Ponte Nova, *Chase 9479* (F, MO, NY, US); Serra da Gramma, E of Araponga, *Chase 9608* (F, GH, MO, US); Lagoa Santa, *Warming s.n.* (NY). RIO DE JANEIRO: Antonio, *Glaziou 5718* (K, P, US); Corcovado, *Chase 9752* (MO); Serra dos Orgãos, *Luetzelburg 6051* (NY). Without locality, *Riedel 2151* (K, US), *Glaziou 16626, 18633* (US), *16628* (P, US), *22612* (G).

*Panicum penicillatum* has a peculiar, bamboo-like habit, with rigid culms leaning on the vegetation and reaching up to 10 m high (T. Filgueiras, pers. comm.). The spikelet also lacks a lower palea.

**21. Panicum peristypum** Zuloaga & Morrone, Novon 1: 113. 1991. TYPE: Brazil. Espírito Santo: Mun. Domingos Martins, Domingos Martins, selva en cerro del Dr. Kautsky, 600–850 m, 7 May 1985, *Zuloaga, Martinelli & Vázquez Avila 2398** (holotype, RB; isotypes, MO, SI, US). Figures 10, 28.

Short-rhizomatous perennial. *Culms* decumbent and rooting at the lower nodes, then erect, ca. 80 cm tall, internodes 7–12 cm long, compressed, striate, glabrous; nodes compressed, glabrous, brownish. *Sheaths* striate, 5–9(–18) cm long, usually shorter than the internodes, glabrous, shiny, the margins membranous, ciliate toward the distal portion. *Ligules* 0.3 mm long, membranous at the base, then shortly ciliate, collar shortly pubescent. *Blades* ovate-lanceolate, 7–15 cm long, 1.5–3 cm wide, cordate, amplexicaulous, acute, velutinous, the lower margins long-ciliate, otherwise ciliate. *Inflorescences* terminal, exserted, *panicles* lax, diffuse, 15 cm long, 8 cm wide; *main axis* sparsely pilose, eglandular, the pulvini pilose, first-order branches alternate or subopposite, the axis of the branches scabrous, flexuous, eglandular; pedicels claviform, flexuous, scaberulous. *Spikelets* narrowly ellipsoid, 2.4–2.5 mm long, 1 mm wide, nonstipitate, glabrous, greenish or tinged with purple, the upper glume and lower lemma subequal. *Lower glume* ovate, 1.2–1.4 mm long, ½ or a little more the length of the spikelet, glabrous, 1–3-nerved, not embracing the upper glume. *Upper glume* 1.9–2.3 mm long, (7–)9-nerved, with manifest nerves, not covering the tip of the upper anthecium. *Lower lemma* glumiform, 2–2.3 mm long, 9-nerved. *Lower palea* lanceolate, 1.7 mm long, 0.4 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 2.2 mm long, 0.8 mm wide, indurate, papillose, lemma crestate, scaberulous; the stamens 3, anthers 1.4 mm long, stigma pink. *Caryopsis* unknown.

*Distribution and ecology:* known only from the type collection in edge of forest in Espírito Santo, Brazil, at 650–850 m.

Related to *P. sciurotoides*, *P. peristypum* has amplexicaulous, 1.5–3-cm-wide leaves, spikelets 2.4–2.5 mm long, and lower palea 1.7 mm long. It differs from *P. sabulorum* and *P. stigmosum* by having narrowly ellipsoid spikelets (obovoid in *P. sabulorum* and *P. stigmosum*), lower glume not embracing the upper glume at its base, and without a short stipe between the lower and upper glume. *Panicum peristypum* also lacks the foliar dimorphism present in *P. sabulorum* and has, as another difference with *P. stigmosum*, amplexicaulous leaves.

The keel structure of *P. peristypum* deserves comment. Two different leaves of *Zuloaga et al. 2398* were examined, and the leaf illustrated (Fig. 10A) clearly has a keel containing three vascular bundles as well as extensive adaxial parenchyma tissue. However, the other leaf from the same plant is without a keel or even a midrib, having a median vascular bundle distinguishable only by its central location in the lamina.

**22. Panicum petropolitanum** Zuloaga & Morrone, Ann. Missouri Bot. Gard. 78: 161. 1991. TYPE: Brazil. Rio de Janeiro: Mun. Petrópolis, Araras, base de Pedra Maria Comprida, saxícola, heliófila, crescendo em beira de Rio, 23 Mar. 1968, *Sucre & Braga 2553* (holotype, RB). Figure 28.

Stoloniferous perennial? *Culms* geniculate, rooting and branching at the lower nodes, then becoming erect, freely branching, 10–25 cm tall, few-noded; internodes 1–4 cm long, cylindric to compressed, hollow, glabrous; nodes compressed, brownish, covered with long hairs to glabrous. *Sheaths* striate, 1.5–5.5 cm long, longer than the internodes, one of the margins long-ciliate with whitish hairs, the other one membranous or with long hairs in the upper portion, the rest of the surface glabrous. *Ligules* membranous-ciliate, ca. 0.2 mm long; collar brownish, glabrous. *Blades* linear-lanceolate, 2–5 cm long, 0.1–0.3 cm wide, flat, glabrous, the margins scaberulous, the apex attenuate. *Inflorescences* terminal, exserted, peduncles to 16 cm long; *panicles* lax, diffuse, 2–4 cm long, 1–3.5 cm wide; *main axis* flexuous, cylindric, glabrous, the pulvini glabrous, first-order

branches alternate, divergent, and distant, the axis of the branches glabrous, eglandular; pedicels triquetrous, scaberulous, 1–7 mm long. *Spikelets* solitary, narrowly ellipsoid, 2.4–2.6 mm long, 0.9 mm wide, glabrous, the upper glume and lower lemma subequal, without a stipe between the lower and upper glume. *Lower glume* 1.8–2 mm long, ¾ the length of the spikelet, lanceolate, not embracing the upper glume, 1(–3)-nerved, the midnerve scabrous toward the apex. *Upper glume* (7–)9-nerved, acute, embracing the lower lemma. *Lower lemma* 9-nerved, embracing the upper anthecium. *Lower palea* lanceolate, 1.5 mm long, 0.3–0.4 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* narrowly ellipsoid, 2.3 mm long, 0.7 mm wide, glabrous, shiny, with simple papillae evenly distributed over its entire surface; lemma apiculate, apicule ca. 0.2 mm long, pilose; lodicules ca. 0.3 mm long, embracing the lower margins of the palea; the stamens 3, anthers 1 mm long. *Caryopsis* ellipsoid, 1.2 mm long, 0.6 mm wide; hilum punctiform, embryo less than ⅓ the length of the caryopsis.

*Distribution and ecology:* Brazil, in mountains of the state of Rio de Janeiro, growing in open and humid places on borders of streams, on rocky soils.

*Panicum petropolitanum* differs from *P. cucaense* in its stoloniferous habit; culms geniculate, few-noded, rooting and branching at the lower nodes and then becoming erect; linear-lanceolate, flat leaf blades; and inflorescence with a peduncle to 16 cm long.

**23. Panicum portoricense** Desv. ex Ham., Prodr.: 11. 1825. *Dichanthelium portoricense* (Ham.) Hansen & Wunderlin, Ann. Missouri Bot. Gard. 75: 1649. 1988. TYPE: Puerto Rico. Without locality, *Desvaux Herb. s.n.* (holotype, P). Figure 27.

*Panicum lancearium* Trin., Gram. Panic.: 223. 1826. TYPE: United States. "Am. bor.," *Trattinick s.n.* (holotype, LE not seen; fragment, US 557424).

*Panicum nashianum* Scribner, U.S.D.A. Div. Agrost. Circ. 7: 79. 1897. *Panicum portoricense* Desv. var. *nashianum* (Scribner) Lelong, Brittonia 36: 267. 1984. TYPE: United States. Florida: Lake County, Eustis, 15–30 Apr. 1894, *Nash 466* (holotype, US 208320).

*Panicum patentifolium* Nash, Bull. Torrey Bot. Club 26: 574. 1899. TYPE: United States. Florida: Lake County, Eustis, 12–31 Mar. 1894, *Nash 72* (holotype, NY; isotypes, MO, US).

*Panicum nashianum* Scribner var. *patulum* Scribner & Merr., U.S.D.A. Div. Agrost. Circ. 27: 9. Dec. 1900. *Panicum patulum* (Scribner & Merr.) A. Hitchc., Rhodora 8: 209. 1906. *Panicum lancearium* Trin. var. *patulum* (Scribner & Merr.) Fernald, Rhodora 36: 80. 1934. *Dichanthelium sabulorum* (Lam.) Gould & Clark var. *patulum* (Scribner & Merr.) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1113. 1978. TYPE: United States. Florida: Manatee County, Bradenton, 3 Sep. 1898, *Combs 1296* (holotype, US 2808982).

*P. wilmingtonense* Ashe, J. Elisha Mitchell Sci. Soc. 16: 86. 1900. TYPE: United States. North Carolina: New Hanover County, near Wilmington, 17 May 1899, *Ashe s.n.* (holotype, NCU not seen; isotype, US).

*P. pauciciliatum* Ashe, J. Elisha Mitchell Sci. Soc. 16: 87. 1900. TYPE: United States. North Carolina: New Hanover County, near Wilmington, 20 May 1899, *Ashe s.n.* (lectotype, NCU not seen; isolectotype, US).

Caespitose perennials, with a basal rosette of broader leaves present or absent. *Culms* decumbent to erect, 4–30 cm tall, freely branching at the upper nodes, internodes cylindric, greenish to purplish, hollow, shortly and densely pilose; nodes shortly pilose. *Sheaths* striate, greenish to purplish, shortly pilose, the margins ciliate. *Ligules* membranous-ciliate, 0.3–0.7 mm long. *Blades* lanceolate, 1–5 cm long, 0.2–0.6 cm wide, flat, subcordate, the apex acuminate, greenish or occasionally purplish, shortly and densely or sparsely pilose on both surfaces, the lower margins long-ciliate or completely ciliate. *Inflorescences* terminal, exserted or partially included in the upper leaves, peduncles cylindric, shortly pilose, to 4 cm long; *panicles* lax, few to multiflowered, 1–4 cm long; *main axis* flexuous, shortly pilose, first-order branches alternate or subopposite, divergent, the axis of the branches and pedicels shortly pilose. Axillary panicles similar to the terminal one. *Spikelets* solitary, obovoid, 1.6–2.4 mm long, 1–1.3 mm wide, shortly hispid, the upper glume and lower lemma subequal, or the upper glume shorter and not covering the upper anthecium. *Lower glume* 0.7–1.1 mm long, ⅓ or more the length of the spikelet, ovate, obtuse to truncate or acute, 1–3-nerved. *Upper glume* 7–9-nerved, obtuse. *Lower lemma* 7-nerved, obtuse. *Lower palea* lanceolate, 0.6–0.8 mm long, 0.4 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* obovoid, 1.2–1.5 mm long, 0.6–0.8 mm wide, pale, smooth, shiny, indurate, with simple papillae, the lemma 7-nerved, shortly apiculate, pilose at the apex. *Caryopsis* obovoid, 0.7–1.3 mm long, 0.5–1 mm wide; hilum punctiform, embryo less than ½ the length of the caryopsis.

*Distribution and ecology:* United States, Mexico to Belize and the West Indies, in moist sandy pinelands, to 1,400 m.

*Additional specimens examined.* BELIZE. Pine Ridge N of aviation field, *Bartlett 11225* (US). CUBA. ISLA DE LA JUVENTUD: vicinity of Siguanea, *Britton et al. 15379* (US). ORIENTE: Sierra Maestra, La Gran Piedra, 1,200

m, *Ekman 8151* (US); Sierra de Nipe, in pineland, between Woodfred and Loma Mensura, *Ekman 15290* (G). PINAR DEL RIO: Arroyo Mántua, Damují, in white sand at Rincón del Prado, *Ekman 11022* (US); Sábalo, in pineland on white sand, *Ekman 11427* (G, US); sandy Sabana de los Remates, *León & Victorin 18702* (US). DOMINICAN REPUBLIC. LA VEGA: La Vega, Cordillera Central, Constanza, Loma del Medio, *Ekman 14094* (G, US); prope Constanza, *von Tuerckheim 3321* (G, US); Montecristi, Lagunas de Cenobí, *Valeur 4* (US). PUERTO RICO. San Juan, Isla Verde, *McKee 10588* (P); track from Manatí to Vega Baja, *Underwood & Griggs 955* (US); Santurce, *Heller 6442* (MO, US); vicinity of San Juan, between Cataño and Guainabo, *Chase 6631* (US); Laguna Tortuguero, *Britton et al. 3853* (MO, US); W end of Laguna Tortuguero, white sand, *Britton & Chardon 6831* (US). UNITED STATES. FLORIDA: Lake County, Eustis, *Nash 1337, 2076* (P).

**24. Panicum pycnoclados** Tutin, J. Bot. 72: 340. 1934. TYPE: Guyana. Kaieteur savanna, Potaro River, 1,100 ft., 20 Aug. 1933, *Tutin 508* (holotype, BM not seen; isotypes, K, US). Figures 11, 28, 34.

*Panicum albociliatum* Swallen, Brittonia 3: 149. 1939. TYPE: Venezuela. Bolívar: Mount Auyan-tepui, 2,200 m, *Tate 1286* (holotype, US 1723625; fragment, VEN 222501; isotype, NY).

*Panicum tiricaense* Swallen, Mem. New York Bot. Gard. 9: 400. 1957. TYPE: Venezuela. Bolívar: upper falls of Río Tirica above summit camp, alt. 1,940–1,950 m, central section, Chimantá Massif, 7 Feb. 1955, *Steyermark & Wurdack 535* (holotype, US 2182126; isotypes, F 1480635, K, NY).

*Panicum tiricaoides* Swallen, Mem. New York Bot. Gard. 9: 401. 1957. TYPE: Venezuela. Bolívar: frequent in thickets along Río Tirica, below summit camp, central section, Chimantá Massif, 1,925 m, 5 Feb. 1955, *Steyermark & Wurdack 475* (holotype, US 2182124; isotypes, G, K, NY).

Perennial. *Culms* leaning on vegetation, decumbent, rooting and branching at the lower nodes, then ascendent to erect, freely branching at the upper nodes, 12–60 cm tall; internodes 3–15 cm long, terete, hollow, glabrous or hirsute, nodes compressed, pubescent with retrorse hairs. *Sheaths* 2–5 cm long, glabrous or hirsute, delicate, the margins long-ciliate. *Ligules* membranous at the base and short to long-ciliate at the apex, (0.2–0.3–)1–1.5 mm long; collar pilose with whitish hairs. *Blades* lanceolate or ovate-lanceolate, 2–4.5(–12) cm long, 0.5–1.8 cm wide, herbaceous, flat, divergent, glabrous or sparsely pilose to densely hispid, cordate, the base amplexicaulous and asymmetric, the apex acute, the margins scabrous, the lower margins long-pilose. *Inflorescences* terminal, exserted, peduncle hispid to glabrous, 6–20 cm long; panicle lax, 3–6(–10) cm long, 1.5–6 cm wide; *main axis* glabrous or hirsute with long papillose-pilose hairs, eglandular, the pulvini pilose or glabrous, first-order branches flexuous, ascendent, alternate or subopposite, occasionally whorled toward the base, glabrescent, eglandular; pedicels pilose toward the distal portion or glabrous, smooth. *Spikelets* ellipsoid, 2.2–3(–3.3) mm long, 0.8–0.9 mm wide, glabrous or pilose, acute and attenuate at the base, with a stipe between the lower and upper glume, upper glume and lower lemma subequal. *Lower glume* ovate-acuminate, (0.7–)1.2–1.8 mm long, ½–¾ the length of the spikelet, 3(–5)-nerved, embracing the upper glume. *Upper glume* 1.9–2.7 mm long, 9-nerved, not covering the apex of the upper anthecium. *Lower lemma* glumiform, 7–9-nerved. *Lower palea* linear-lanceolate, 1.5–1.8 mm long, 0.3 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 1.8–2.1 mm long, 0.8 mm wide, indurate, pale, lemma slightly crested at the apex, scabrous and pilose; stamens 3, anthers 0.8 mm long. *Caryopsis* ellipsoid, 1.5 mm long, 0.8 mm wide, hilum punctiform, embryo ⅓ the length of the caryopsis.

*Distribution and ecology:* Ecuador, Peru, Venezuela, Guyana, Surinam, and Brazil, on forest edges, often leaning on vegetation, or in open places, between 500 and 2,600 m.

*Additional specimens examined.* BRAZIL. BAHIA: Rui Barbosa, *Almeida 22* (US); Serra do Tombador, NW of Jacobina, on BR-234 to Ouro Branco, 950 m, *Harley et al. 16634* (K); Serra do Sincorá, Lagoa Encantada, 19 km NE of Ibicoara, *Harley et al. 15783* (CEPEC, K, US). CEARA: Campo Grande, *Swallen 4531* (US). RORAIMA: without locality, *Rondôn s.n.* (RB 110790). ECUADOR. LOJA: between La Toma and Loja, 1,800–2,600 m, *Hitchcock 21420* (US). GUYANA. Kaieteur Plateau, *Maguire & Fanshawe 23446* (K, NY); vicinity of Kaieteur Falls and along W rim of Potaro Gorge, ca. 1,400 ft., *Cowan & Soderstrom 1891* (K, NY, P). PERU. CAJAMARCA: Cutervo, a 7 km sobre la carretera Cutervo–Socota, *Sánchez-Vega 2295* (SI). SURINAM. 5 km E of Lucie Rivier, *Irwin et al. 55684* (K, SI, US); 14 km N of Lucie Rivier, *Maguire et al. 54280* (US). VENEZUELA. AMAZONAS: Dpto. Atabapo, Cerro Huachamacari, base of main wall and slope below it, E side, 800–1,300 m, forest, 3°49′N, 65°43′W, *Liesner 25867* (MO). ANZOATEGUI: Distr. Freites, burro trail between San Durnal and Los Pajaritos, *Davidse & González 19792* (VEN); Cerro Peonia, above Los Pajaritos, 31 km NE of Bergantín and N of Mundo Nuevo, Serranía of Turimiquire, 1,400–1,700 m, *Davidse & González 19850* (MO, VEN), *19914A* (MO, VEN); Distr. Libertad, ridges and tops of Montañas Negras, along the Sucre and Anzoátegui border, 20 airline km NE of Bergantín, NE of Buenos Aires, Serranía de Turimiquire, 2,000 m, *Davidse & González 19563* (MO). BOLIVAR: Gran Sabana, formación Roraima, a lo largo del Río Aponguao, cerca del km 146 al S de El Dorado, 1,350–1,400 m, *Steyermark et al. 104200* (COL, US); la Gran Sabana, 49 km W of the intersection of the main road to Santa Elena and road to Cabanayén, 1,360 m, *Davidse et al. 4749* (MO, US, VEN), *4783a* (MO, SI, VEN); la Gran Sabana, ca. km 167, S of El Dorado along Hwy. to Santa Elena, 24 km S of La

FIGURE 34. *Panicum pycnoclados.*—A. Habit.—B. Detail of clasping base of the blade.—C. Spikelet, lower glume view.—D. Spikelet, lateral view.—E. Spikelet, upper glume view.—F. Lower palea.—G. Upper anthecium, lemma view.—H. Upper anthecium, palea view.—I. Detail of apex of the lemma.—J. Upper palea with lodicules, anthers, and stigma.—K. Caryopsis, embryo view.—L. Caryopsis, hilum view. (All based on *Steyermark 87974.*)

Ciudadela, *Davidse 4763* (MO, SI, VEN); a 12 km al N de La Ciudadela, Gran Sabana, 1,400 m, 5°50′N, 61°27′W, *Zuloaga et al. 4474* (MO, SI, VEN); entre Piedra de la Virgen y la parte alta de la Escalera, carretera a la Gran Sabana, 500–1,400 m, 6°0′N, 61°25′W, *Zuloaga et al. 4404** (MO, SI, VEN); Distr. Piar, Chimantá Massif, 1,600–1,700 m, *Steyermark 75642* (NY, US), *128196* (SI); Sierra Imataca, Río Toro, between Río La Reforma and Puerto Rico, N of El Palmar, 200 m, *Steyermark 87974* (NY, US, VEN); Meseta del Jaua, Cerro Jaua, cumbre, 4°48′N, 64°34′W, *Steyermark et al. 109377* (NY); Jaua, sector centro-meridional, cabeceras del Río Marajano, 4°48′N, 64°32′W, *Huber 13043, 13046* (MO).

Zuloaga & Judziewicz (1991) mentioned that the specimen *Tutin 651* is marked as type of *P. pycnoclados* in BM.

This is one of the species of *Panicum* found at higher elevations, being present in Ecuador to 2,600 m.

Swallen (1939, 1957) described three species from Venezuela: *P. albociliatum*, *P. tiricaense*, and *P. tiricaoides*. No morphological differences were observed between these species and *P. pycnoclados*.

*Panicum pycnoclados* is characterized by having asymmetrical, lanceolate or ovate-lanceolate leaves and spikelets 2.2–3(–3.3) mm long with a conspicuous internode between the lower and upper glume. While most of the specimens of *P. pycnoclados* examined have glabrous spikelets, some populations have spikelets with short hairs.

*Panicum pycnoclados* shows close affinities to *P. stipiflorum*, and the latter species may represent a variant of *P. pycnoclados*. *Panicum pycnoclados* has spikelets with the lower glume ½–¾ the length of the spikelet, and blades with only the lower margins pilose. *Panicum stipiflorum* has spikelets with the lower glume usually ½ the length of the spikelet and blades with long-ciliate margins.

Anatomically, the specimen studied has a definite keel that is structurally distinguishable from the other first-order vascular bundles due to the presence of additional sclerenchyma tissue in the form of adaxial and abaxial girders (Fig. 11A). The cushion-based macrohairs of *P. pycnoclados* are of interest, as this hair type is not common in the section. The hair bases are clearly sunken between numerous raised and modified epidermal cells which form the cushion (Fig. 11B). The hairs themselves are also much thicker than the needlelike hairs that occur on other species such as *P. cumbucana* (Fig. 6C), *P. hebotes* (Fig. 9A–D), and *P. peristypum* (Fig. 10C, D). The thick, cushion-based macrohair type is best developed in *P. pycnoclados*, although similar hairs do occur in *P. viscidellum* (Fig. 19), some specimens of *P. acuminatum* (Fig. 3E, F), and near the leaf blade margin in *P. davidsei* and *P. sabulorum* (Fig. 12A).

**25. Panicum sabulorum** Lam., Encycl. 4: 744. 1798. *Dichanthelium sabulorum* (Lam.) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1112. 1978. TYPE: Uruguay. Montevideo: Montevideo, *Commerson s.n.* (holotype, P; fragment, BAA; isotypes, R, US). Figure 12.

Short-rhizomatous perennials, with two different kinds of *culms*: young culms simple, erect, with broad, cordate, lanceolate leaves; older culms erect to decumbent, occasionally rooting and profusely branching at the lower and upper nodes, to 1 m long, with leaves smaller than those of the primary culms; internodes hollow, cylindric, hirsute, nodes densely pilose to glabrous, dark. *Sheaths* 2.5–6 cm long, hirsute to glabrous, the margins ciliate, glands present or absent, more conspicuous toward the distal portion. *Ligules* membranous-ciliate, 0.4–1.1 mm long. *Leaves* lanceolate, 1–9(–15) cm long, 0.2–1.4(–2) cm wide, flat, the base subcordate or cordate, amplexicaulous, the apex acuminate, rigid to herbaceous, hispid, with short, stiff hairs or with papillose-pilose hairs, or glabrous, the lower margins long-ciliate, otherwise scabrous, the midnerve inconspicuous. Primary *inflorescences* lax, diffuse, few- to multiflowered, *panicles* 2–10 cm long, 2–8 cm wide; *main axis* hirsute or glabrous, glandular or eglandular, first-order branches alternate, divergent, the axis of the branches long-hirsute to scabrous and glandular or eglandular; pedicels claviform, hirsute, glandular or eglandular; axillary panicles similar to the terminal one, smaller. *Spikelets* obovoid, biconvex, 1.9–3 mm long, 0.9–1.4 mm wide, paired or solitary, shortly stipitate, greenish and tinged with purple, hirsute to glabrous, glumes and lower lemma with manifest nerves. *Lower glume* ½–¾ the length of the spikelet, 3–5-nerved, the nerves anastomosing toward the apex, ovate, obtuse to acute and embracing the upper glume on its base. *Upper glume* 7–9-nerved, obtuse, not covering the apex of the upper anthecium. *Lower lemma* glumiform, 7–9-nerved. *Lower palea* ovate, 1.6 mm long, 0.8 mm wide, hyaline, the margins short-ciliate; lower flower male or absent. *Upper anthecium* broadly ellipsoid, 1.8–2.5 mm long, 0.7–1.2 mm wide, stramineous, shiny, shortly apiculate, with simple papillae in regular rows; lemma 5-nerved. *Caryopsis* broadly ellipsoid, 1.5 mm long, 1 mm wide; hilum punctiform, embryo less than half the length of the caryopsis.

KEY TO THE VARIETIES

1. Leaf blades clasping the culm 25c. var. *cordatum*
1. Leaf blades not clasping the culm ..... 2

2. Spikelets (2.2–)2.4–3 mm long, pilose; blades pilose; plants growing in open, dry places ..... 25a. var. *sabulorum*
2. Spikelets 1.9–2.3(–2.6) mm long, glabrous or sparsely pilose; blades glabrous; plants growing on forest edges in humid places ..... 25b. var. *polycladum*

**25a. Panicum sabulorum** var. **sabulorum**. Figure 32.

*P. acutatum* Steudel, Syn. Pl. Glumac. 1: 86. 1853. TYPE: Chile. Concepción: Concepción, *D'Urville s.n.* (holotype, P; fragments BAA, US 80445).

*Panicum latiglume* Doell in C. Martius, Fl. Bras. 2(2): 257. 1877. *Panicum latiglume* var. *villosum* Doell in C. Martius, Fl. Bras. 2(2): 257. 1877. *Panicum latiglume* Doell f. *villosum* (Doell) E. Ekman, Ark. Bot. 13(10): 28. 1913. *Panicum latiglume* Doell f. *genuinum* (Doell) E. Ekman, Ark. Bot. 13(10): 28. 1913, nom. illeg. TYPE: Brazil. Santa Catarina: Isla de Santa Catarina, *Gaudichaud 90* (isotype, P; fragment, US 80869).

*Panicum latiglume* Doell var. *decalvatum* Doell in C. Martius, Fl. Bras. 2(2): 257. 1877. *Panicum latiglume* Doell f. *decalvatum* (Doell) E. Ekman, Ark. Bot. 13(10): 28. 1913. TYPE: Brazil. Santa Catarina: Isla de Santa Catarina, *Gaudichaud 91* (fragment, US 80869).

*Panicum fultum* Hackel, Repert Spec. Nov. Regni Veg. 6: 342. 1909. SYNTYPES: Uruguay. Montevideo: Montevideo, arenales de la Barra de Santa Lucía, *Arechavaleta s.n.* (syntypes, W, G, BAA). Paraguay. Cordillera: in campis prope Caraguatay, *Hassler 3124* (syntypes, G, NY, W, fragment, BAA).

*Distribution and ecology:* southern Brazil, Argentina, Paraguay, and Chile; found in open places on sandy soils.

*Selected specimens cited.* ARGENTINA. BUENOS AIRES: Balcarce, *Hunziker 2166* (SI). CORRIENTES: La Cruz, *Burkart 7943* (SI), *Parodi 12364* (US); ruta nac. 12, 20 km E de Ituzaingó, *Zuloaga et al. 3231* (SI). ENTRE RIOS: arroyo El Palmar, *Burkart & Crespo 22927* (SI), *Zuloaga & Morrone 3857* (MO, SI); Colonia Ayuí, *Zuloaga & Morrone 3852* (MO, SI); Colón, Palmar, *Burkart et al. 23267* (SI); ruta 12, desvío a Holt, arroyo El Cuartillo, *Zuloaga 3864* (MO, SI). CHACO: Isla del Cerrito, *Krapovickas & Cristóbal 20048* (CTES). BRAZIL. PARANA: Colônia Orleàs, Curitiba, *Dombrowski 1958* (CTES); Mun. 4 Barras, Rio Taquari, próx. Estr. Graciosa, *Hatschbach 35525* (K). RIO DE JANEIRO: Petrópolis, Carangola, *Góes & Dionisio 417* (US). RIO GRANDE DO SUL: Taimbesinho, prope São Francisco de Paula, *Rambo 54532* (US); Rio Grande, *Swallen 9252* (US); entre São Lourenço e Camaqua, *Pereira 6811* (RB); Bagé, Hulha Negra, *Allem & Vieira 1809* (ICN, SI); Sta. Maria, Est. Experimental, 23 Nov. 1955, *Camargo s.n.* (SI); Osório, estrada Pasinhos a Osório, 7 km antes do entroncamento com a BR-101, margem da Lagoa dos Barros, *Valls et al. 2308* (CTES); Lages, *Swallen 8140* (US). SANTA CATARINA: Sombrío, *Reitz 1978* (NY); Serra dos Ilheos, *Smith & Klein 15464* (NY, SI); Ubatuba, *Hans 317* (SI); without locality, *D'Urville s.n.* (W). SÃO PAULO: Cananeia, Ilha do Cardoso, Praia do Marujá, *da Silva 249* (MO); São Paulo, Parque do Estado, *Sendulsky 768* (SI), *842* (SI, SP); Santos, *Sendulsky 739* (SI, SP). CHILE. CONCEPCION: Concepción, *D'Urville 1821* (P), *Gay s.n.* (P). MAULE: without locality, *Fuentes s.n.*, Dec. 1911 (W). PARAGUAY. PARAGUARI: Paraguarí, *Balansa 8*, (G, K, P); Cordillera de Piribebuy, au desus de Mbatobí, 1 Nov. 1883, *Balansa 4202* (P). URUGUAY. CANELONES: Ruta Interbalnearia Km 51, Arroyo Solís Chico, *Dubcovsky 834, 835, 836, 837* (all SI); Carrasco, *Burkart 19982* (SI), *Osten 6917* (W), *Herter 324* (G, MO, NY, SI). MONTEVIDEO: Montevideo, *Arechavaleta 144* (W), *Montoro 2667* (P); prés Montevideo, *D'Orbigny 8* (W). ROCHA: La Paloma, *Zuloaga & Deginani 1081* (SI). SALTO: Granja Catáneo, *Rosengurtt B-6217* (SI). TACUAREMBO: Camino a Ribera, a 32 km de Tacuarembó, *Cabrera & Zuloaga 32424, 32425* (SI).

In this variety the spikelets are pilose, (2.2–)2.4–3 mm long, the axis of the inflorescence is hirsute, and the blades are rigid and hirsute.

**25b. Panicum sabulorum** var. **polycladum** (E. Ekman) Palacios, in Burkart, Fl. Ilustr. Entre Ríos, Colec. Cient. INTA 6(2): 316. 1969. *Panicum polycladum* E. Ekman, Ark. Bot. 11(4): 24. 1912. TYPE: Argentina. Misiones: Bonpland, 27 Jan. 1908, *Ekman 651* (holotype, S; fragment, US 80923; isotype, CORD). Figure 32.

*Panicum demissum* Trin., Spec. Gram. 3: pl. 319. 1832. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Martius s.n.* (holotype, LE; fragment, US 557430).

*Panicum ramosissimum* Trin., Mem. Acad. St. Petersb. VI. Sci. Nat. 1: 312. 1834. TYPE: Brazil. Without locality, *Sellow s.n.* (holotype, LE; fragment, US 974731).

*Panicum pencanum* Philippi, Anal. Univ. Chile 93: 713. 1896. TYPE: Chile. Concepción: Concepción, 1888, *Philippi s.n.* (isotype, CORD; fragment, BAA, US).

*Panicum deltae* L. Parodi ex Burkart, Bol. Soc. Argent. Bot. 12: 291. 1968. TYPE: Argentina. Buenos Aires: Delta del Paraná inferior bonaerense, arroyo Chaná Miní, 14 Jan. 1923, *Parodi 4928* (holotype, SI; isotypes, BAA, US 1160950).

*Distribution and ecology:* found from the states of Minas Gerais and Rio de Janeiro to southern Brazil; also in Paraguay, Uruguay, Argentina, Bolivia, and Chile. Plants grow in shady and wet areas, on forest edges, to 1,500 m.

*Selected specimens cited.* ARGENTINA. BUENOS AIRES: Punta Lara, *Zuloaga & Deginani 1891, 3085* (SI), *3859, 3861* (SI); Cerro La Peregrina, 20 km N of Mar del Plata, *Eyerdam et al. 23678* (MO, SI, US); Escobar, Paraná de Las Palmas, *Zuloaga & Morrone 3079, 3860* (SI), *4543, 4544* (MO, SI). CORDOBA: W of Tanti at Rancho Alegre, *Renvoize 3743* (SI); between Cerro Blanco and La Hollada, ruta nac. 20, km 767, *Solomon 4091* (MO). CORRIENTES: Puente Pesoa, *Quarín 1744* (CTES, SI); ruta nac. 12, 20 km E de Ituzaingó, *Zuloaga et al. 3228* (SI); Cuay Grande, *Zuloaga & Deginani 554* (SI); Estancia Santa Teresa, *Pedersen 2997* (P). ENTRE RIOS: Nueva Escocia, *Bacigalupo et al. 871* (SI); ruta 14 y Río Gualeguaychú, 4 km al N, *Bacigalupo et al. 579*

(SI); San José de Feliciano, Arroyo Feliciano, *Bacigalupo et al. 696* (SI). FORMOSA: without locality, *Kermes 346* (SI). JUJUY: Sierra de Zapla, Mina 9 de Octubre, *Cabrera et al. 32004* (SI); Santa Bárbara, *Venturi 9545* (SI, US, W), *9691* (US). MISIONES: Villa Venecia, *Renvoize et al. 3034* (P, SI); casa de Horacio Quiroga, *Zuloaga et al. 3191* (MO, SI); La Granja, Posadas, *Ekman 645* (G, US); 15 km de San Javier, *Zuloaga et al. 1972** (SI); entre San Pedro y Puerto Piray, km 76, *Zuloaga et al. 2060** (SI); San Antonio, *Zuloaga et al. 2128** (SI). SALTA: Cerro Pelado Chiquito, Parque Nac. El Rey, *Malmierca 2006* (SI); Depto. Rosario de Lerma, Campo Quijano, *Venturi 8428* (US). BOLIVIA. COCHABAMBA: Comarapa to Cochabamba, *Renvoize & Cope 4072* (K, US). SANTA CRUZ: entre Comarapa y Pojo, *Zuloaga et al. 1579* (SI). BRAZIL. ESPIRITO SANTO: Serra do Caparaó, *Chase 9680* (MO), *9730* (US), *9731* (US, W). MINAS GERAIS: Serra do Itabirito, ca. 50 km SE of Belo Horizonte, *Irwin et al. 19715* (MO, NY, US); Barbacena, Serra Mantiqueira, *Chase 8646* (NY, US), *8674* (NY, US); Mun. Itamonte, Parque Nacional de Itatiaia, *Zuloaga et al. 2380** (SI). PARANA: Passa Vinte, *Clayton 4269* (K, NY, US); Mun. Jaguariaiva, Fazenda Samanbaia, *Hatschbach 35451* (K); 2 km E of Cascavel along highway BR-277 to Curitiba, *Davidse et al. 11255* (MO, SI, US). RIO GRANDE DO SUL: Santa Vitoria do Palmar, *Swallen 7406* (US); Tenente Portela, *Valls et al. 1780* (CTES, US); Nova Petrópolis, km 100 da BR-116, ao N da ponte sobre o Rio Caí, *Valls et al. 1664* (CEN, ICN, SI), *1665* (ICN, SI). RIO DE JANEIRO: Corcovado, *Chase 8159* (MO, NY); Patí do Alferes, *Sucre et al. 9087* (RB); Parque Nacional Itatiaia, picada Macieiras, *Zuloaga et al. 2352** (RB, SI, US), *Chase 8267* (RB, US), *8268* (US); Parque Nac. Itatiaia, Rio Campo Belho, *Zuloaga et al. 2361** (RB, SI, US); Serra dos Orgãos, 16 km S of Itaipara, *Davidse et al. 11422* (MO). SANTA CATARINA: 4 km S of Xanxeré, *Smith & Klein 13066* (K, NY, SI); W of Chapecó on road to Guatambú, *Smith & Reitz 12534* (K, R, US); Mun. Ponte Serrada, 2 km S of Paraná line, fazenda, *Smith et al. 15680* (US); Mun. São Joaquim, Rio Lava Tudo, *Smith & Klein 15896* (K, SI, US); 10 km S of São Joaquim, *Smith & Reitz 14305* (K, NY, SI, US). SÃO PAULO: Campos do Jordao, Serra Mantiqueira, *Chase 9894* (US); city of São Paulo, Agua Funda, *Eiten & Eiten 6236* (MO). CHILE. Taleamavida, *Barros 291* (SI). MAULE: ad rivulos pr. Constitución, *Reiche s.n.* (W). PARAGUAY. Encarnación, *Pavetti & Rojas 10855* (US). CAAGUAZU: in viciniis Caaguazú, *Balansa 4a* (K, P), *Hassler 9212* (G, K, NY, US). CORDILLERA: Eusebio Ayala, *Schinini 2423* (CTES), *2583* (CTES, SI). GUAIRA: Villa Rica, *Balansa 5* (G), *5a* (P). URUGUAY. CANELONES: Toledo, *Osten 20083* (US). FLORIDA: Río Yí y Arroyo Mansavillagra, *Rosengurtt B-739* (US); La Palma, *Herter 1153* (US). MALDONADO: Cerro Pan de Azucar, *Rosengurtt B-2722* (US). MONTEVIDEO: Montevideo, Barra del Santa Lucía, *Arechavaleta 267* (US); Montevideo, balneario Carrasco, *Osten 6511* (SI). ROCHA: Parque San Miguel, *Rosengurtt & Del Puerto 9253* (US). SAN JOSE: Río Santa Lucía, próximo al pueblo "25 de Agosto," *Rosengurtt B-247* (US). SORIANO: Isla Redonda, *Berrio 6350* (W). TACUAREMBO: Gruta de los Cuervos, *Cabrera & Zuloaga 32393* (SI).

*Panicum sabulorum* var. *polycladum* usually grows in humid and shady places, on forest edges or streams. It differs from variety *sabulorum* by having smaller spikelets (1.9–2.3(–2.6) mm long) that are glabrous or with scattered hairs toward the apex; herbaceous and usually glabrous blades; and panicles with the main axis and branches commonly glandular.

*Glaziou 4305*, from Rio de Janeiro, Brazil, was cited by Doell (1877) as *P. nodiflorum* Lam. (= *P. dichotomum* L. var. *dichotomum*).

**25c. Panicum sabulorum** var. **cordatum** Zuloaga & Morrone, Novon 1: 117. 1991. TYPE: Brazil. Paraná: Carvalho, *Dusén 13336* (holotype, US; isotype, W). Figure 32.

*Additional specimens examined.* BRAZIL. PARANA: Serrinha, *Jönson 1076a* (US), *Dusén 15596* (NY, SI, US); Trancheira, *Jönson 1099a* (US). SANTA CATARINA: Pilões, 200 m, *Reitz & Klein 3225* (NY, US); Mun. Praia Grande, *Valls 10087* (CEN, SI).

In this variety the spikelets are glabrous, 2–2.2 mm long; manifest glands are present on the glabrous sheaths and axis of the inflorescences; and the leaf blades are amplexicaulous, cordate, asymmetrical at base, glabrous and up to 15 cm long and to 2 cm wide.

**26. Panicum sciurotis** Trin., Gram. Panic. 228. 1826. *Dichanthelium sciurotis* (Trin.) Davidse, Novon 2: 104. 1992. TYPE: Brazil: "V. sp. Brasil," *Chamisso s.n.* (holotype, LE). Figure 28.

*Panicum rostellatum* Trin., Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, Sci. Math., Seconde Pt. Sci. Nat. 3(2): 288. 1834. TYPE: Brazil. Bahia: "In arenosis prope Ilheos (Brasil) Sep. 1821," without collector, 232 (holotype, LE; fragment, US 974732).

*P. cordifolium* Steudel, Syn. Pl. Glumac. 1: 85. 1853, non Desv. 1831. *Panicum sciurotis* Trin. var. *breviglume* Doell in C. Martius, Fl. Bras. 2(2): 250. 1877. TYPE: Paraguay. Without locality, *Rengger s.n.* (holotype, P).

*P. trichopiptum* Steudel, Syn. Pl. Glumac. 1: 85. 1853. TYPE: Brazil. Bahia: without locality, *Salzmann s.n.* (lectotype, P; fragment, US 2903508).

*P. diffusulum* Salzm. ex Steudel, Syn. Pl. Glumac. 1: 89. 1853. TYPE: Brazil. Bahia: without locality, in sabulosis umbrosis, *Salzmann 684* (holotype, P; fragments, US 967933, 974705, 2903510; isotypes, G, K, MO, P, W).

*P. sciurotis* Trin. var. *molliusculum* Doell in C. Martius, Fl. Bras. 2(2): 250. 1877. TYPE: Brazil. "In Insula S. Catharinae," *Chamisso s.n.* (lectotype, here designated, LE).

Annual. *Culms* geniculate, decumbent, rooting and branching at the lower nodes, then becoming erect, 5–25 cm tall; internodes hollow, compressed, hirsute, 2–8 cm long; nodes dark, densely pilose with retrorse whitish hairs. *Sheaths* striate, 1–5 cm long, hirsute, with long whitish hairs, the margins ciliate. *Ligules* membranous-ciliate, ca. 0.4 mm long; collar pilose, brownish. *Blades* ovate-

lanceolate, 1.5–9 cm long, 0.8–2.8 cm wide, herbaceous, flat, hirsute, papillose-pilose with short, rigid hairs, the base amplexicaulous, the margins ciliate, the midnerve inconspicuous. *Inflorescence* terminal, exserted; peduncle 5–7.5 cm long, flexuous, hirsute; *panicles* lax, diffuse, 2–7 cm long, 1–5 cm wide; *main axis* flexuous, papillose-pilose with long hairs; pulvini pilose; first-order branches divergent, alternate or opposite, the axis of the branches flexuous, smooth, glabrous or with scattered long hairs; pedicels smooth, glabrous; axillary panicles present, similar to the terminal one. *Spikelets* solitary, ellipsoid, 1.5–1.7 mm long, 0.7–0.8 mm wide, hirsute, with short hairs, the upper glume and lower lemma subequal or the upper glume shorter, the nerves inconspicuous. *Lower glume* 0.3–0.4 mm long, ¼ or less the length of the spikelet, nerveless, truncate, not embracing the upper glume at the base. *Upper glume* obtuse, not covering the apex of the anthecium, 5(–7)-nerved, the nerves anastomosing, obtuse. *Lower lemma* glumiform, obtuse, slightly inflated at the base, 5-nerved, the nerves anastomosing toward the distal portion. *Lower palea* lanceolate, 0.9 mm long, 0.2 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 1.4–1.5 mm long, 0.5–0.7 mm wide, glabrous, smooth and shiny, short-apiculate, with simple papillae all over its surface. *Caryopsis* obovoid; hilum punctiform; embryo ⅓ the length of the caryopsis.

*Distribution and ecology:* restricted to northeastern Brazil, where it grows in sandy soils, in open places or forest edges.

*Additional specimens examined.* BRAZIL. BAHIA: Bahia, *Chase 7901* (F, RB, SI, US, W); Cruz das Almas, *Pinto 941* (US). CEARA: Campo Grande, *Swallen 4539* (RB, SI, SP, US); Campo Salles to Crato, *Swallen 4303* (K, R, SP); Serra do Araripé, *Luetzelburg 26101* (M, US); Serra do Araripé, Novo Exú, *Luetzelburg 26141* (M). PERNAMBUCO: Carvarú, *Tenorio 66-197* (US); Garánhuns, *Chase 7791* (US); vicinity of Recife, *Chase 7732 1/2* (US); Recife, *Tavares 788* (US). RIO GRANDE DO NORTE: Natal, *Swallen 4677* (SP, US); Nova Cruz to Montanhas, *Swallen 4823* (RB, SP, US); entre Parnamirim e São Jose de Mipibú, *Emygdio 1663* (R, US); without locality, *Riedel s.n.* (K, M, P, US 974737).

The type locality of the species, Santa Catarina, Brazil, is probably erroneous, since *P. sciurotis* has only been found in northeastern Brazil, in Ceará, Pernambuco, Bahia, and Rio Grande do Norte. The same is probably true for the type material of one of its synonyms, *P. cordifolium*, which was originally cited from Paraguay.

*Panicum sciurotis* differs from *P. sciurotoides* in having spikelets with the lower glume nerveless and truncate; upper glume and lower lemma 5(–7)-nerved with the nerves not manifest; upper anthecium inserted laterally in relation to the axis of the rachilla; and lower lemma inflated at the base.

*Panicum litigosum* Steudel, a species often associated with *P. sciurotis*, is a synonym of *P. brevifolium* L., an African species in Bahia, Brazil.

**27. Panicum sciurotoides** Zuloaga & Morrone, Novon 1: 1. 1991. *Dichanthelium sciurotoides* (Zuloaga & Morrone) Davidse, Novon 2: 104. 1992. TYPE: Brazil. Minas Gerais: Distr. Diamantina, Christais, near Corriga Duas Pontes, 1,160 m, 13 May 1931, *Mexía 5819* (holotype, MO; isotypes, G, K, M, P, R). Figures 14, 28.

Annual. *Culms* decumbent, geniculate, rooting and branching at the lower nodes, erect portion 10–85 cm tall, branching at the upper nodes; internodes 2.5–11.5 cm long, terete, hollow, hispid to glabrous; nodes dark, compressed, densely pilose with retrorse whitish hairs. *Sheaths* striate, 3–6.5 cm long, sparsely papillose-pilose to glabrous, the margins ciliate or one margin ciliate and the other one membranous. *Ligules* membranous-ciliate, small, surmounted by long hairs at the base of the blade; collar pilose. *Blades* ovate-lanceolate, 3–10 cm long, 0.8–2 cm wide, flat, the base cordate, clasping and asymmetric, either densely hirsute with short to long appressed tuberculate hairs or short-hispid on the abaxial surface, or glabrous, the margins ciliate toward the base, otherwise scabrous. *Inflorescence* terminal, lax, diffuse, pyramidal, 2.5–9 cm long, 1.5–8.5 cm wide; *main axis* flexuous, hirsute, with long papillose-pilose hairs; branches alternate, flexuous, the axis of the branches smooth, glabrous; pedicels glabrous. *Spikelets* solitary, narrowly ellipsoid, 1.5–1.9 mm long, 0.5–0.7 mm wide, greenish, short-hispid, the upper glume and lower lemma subequal. *Lower glume* ovate, 0.4–0.9 mm long, usually ⅓–½ or more the length of the spikelet, acute to truncate, 1–3(–7)-nerved. *Upper glume* 7–9(–11)-nerved, not embracing the lower lemma. *Lower lemma* glumiform, 7–9-nerved, acute, not inflated at the base. *Lower palea* lanceolate to truncate, 0.7–1 mm long, 0.2–0.3 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 1.2–1.7 mm long, 0.4–0.6 mm wide, smooth, shiny, short-apiculate, with simple papillae over its entire surface. *Caryopsis* 1.1 mm long, 0.7 mm wide.

*Distribution and ecology:* widely distributed from Belize and Panama to Bolivia and Brazil; common on forest edges, with the culms straggling in low vegetation, often in disturbed and open places in sandy soils; from 100 to 1,400 m.

*Selected specimens cited.* BELIZE. EL CAYO: ca. 3 mi. S of Grano de Oro on road between Millionario and La Flor, *Croat 23391, 23398A* (MO). BOLIVIA. LA PAZ: Hacienda Canana, sobre el camino a Tipuani, *Buchtien 7115* (BAA, G, US), *7116* (MO); Hacienda Simaco sobre el camino a Tipuani, *Buchtien 5319* (M, MO, US). BRAZIL. ALAGOAS: Porto de Pedras, Fazenda Canada, *Campelo 1444* (CTES). BAHIA: Bom Jesus, *Luetzelburg 135a* (M); São Bento das Lages, *Luetzelburg 133* (K, M); 12 km N of Cachoeira, 225 m, *Chase 8082* (MO, US); Serra do Tombador, NW of Jacobina, on BR 234 highway to Ouro Branco, *Harley et al. 16636* (CEPEC, K, US); Serra da Agua de Rega, ca. 27 km N of Seabra, road to Agua de Rega, 1,000 m, *Irwin et al. 31023* (MO). CEARA: Barra do Cocó, *Black 55-18336* (IAN); Praia Náutica de Fortaleza, *Black 55-18347* (IAN). ESPIRITO SANTO: Alfredo Chaves, Vila São Bento de Uranio, *Zuloaga et al. 2409* (RB, SI, US); Santa Teresa, Reserva Biologica de Nova Lombardía, Picada da Cachoeira, *Zuloaga et al. 2427* (RB, SI, US). MINAS GERAIS: Diamantina, Serra de San Antonio, *Chase 10373* (US); ca. 1 km S of São Pedro do Suaçui along Hwy. MG-3, 520 m, *Davidse et al. 11495* (MO); Juiz de Forá, Morro do Imperador, *Chase 8571* (US); abandoned diamond mines, steep slopes of Rio Jequití, ca. 15 km E of Diamantina, *Irwin et al. 27933* (MO, P); ca. 15 km N of São Joao da Chapada, *Irwin et al. 28151* (F, K, MO, UB, US); Serra do Espinhaço, ca. 8 km E of Diamantina, *Irwin et al. 27666* (K, MO, UB, US). PARANA: Paranaguá, *Dombrowski 277* (K, US); Pinheirinho, Mun. Antonina, *Hatschbach 14758* (K, US). PERNAMBUCO: Dois Irmaos, vicinity of Pernambuco, *Chase 7732* (MO, US); SW of Garanhuns, 300–400 m, *Chase 7828* (MO). RIO DE JANEIRO: Monte Serrat, Serra da Itatiaia, *Chase 8246* (IAN, MO, US); Parque Nac. Itatiaia, Picada Macieiras, *Zuloaga et al. 2349** (MO, RB, SI, US), *2354** (RB, SI, US). SANTA CATARINA: Vila Velha, arredores, *Paciornik 117* (K); without locality, *D'Urville s.n.* (P), *Schenck 229* (W). SÃO PAULO: Cananeia Island, 1 km NE of city along E shore of island, *Clayton & Eiten 4743* (K). ECUADOR. EL ORO: between La Chonta and Portovelo, *Hitchcock 21211* (US). TUNGURAHUA: Baños, *Pachano 228* (US). GUYANA. Forest along Potaro River, 4 mi. above Kaieteur Falls, *Cowan & Soderstrom 2109* (K, NY, P, US). FRENCH GUIANA: Galbao Mt., 650 m, *de Granville et al. 8966* (CAY, P, US). PANAMA. COCLE: along continental divide near sawmill above El Copé, *Knapp 3822* (SI). VENEZUELA. BOLIVAR: 12 km al N de La Ciudadela, Gran Sabana, 5°50′N, 61°27′W, *Zuloaga et al. 4475** (MO, SI, VEN); Salto El Dante, 35 km N of La Ciudadela on way down from La Gran Sabana, along highway to El Dorado, *Davidse 4951* (MO, SI, VEN); entre Piedra de la Virgen y la parte alta de la Escalera, carretera a la Gran Sabana, 60°01′N, 61°25′W, *Zuloaga et al. 4399* (MO, SI, VEN). FALCON: cerca de Maraparari, *Lasser & Foldats 3005* (VEN). YARACUY: 7.5 km N of Salom, cloud forest, 10°15′N, 68°29′W, *Liesner & Steyermark 12373* (MO); 5 km N of Salom, transition between savanna and forest, *Davidse et al. 20674* (MO).

*Panicum sciurotoides* is related to *P. sciurotis* Trin., from which it differs in having the lower glume ⅓–½ or more the length of the spikelet and 1–3(–7)-nerved; the upper glume 7–9(–11)-nerved; the lower lemma 7–9-nerved and not inflated at base; and the upper anthecium inserted basally. *Panicum viscidellum* differs from *Panicum sciurotoides* in its pseudoligule composed of long hairs.

Anatomically, all specimens examined are very similar in leaf anatomy (Fig. 14). The keel of this species is distinctive, containing only a single vascular bundle (Fig. 14A). The asymmetrical, S-like nature of the lamina on either side of the keel is of particular interest, as this structure does not occur in any other taxon of section *Dichanthelium*, yet is common in section *Cordovensia*, also of subgenus *Dichanthelium*.

Large-spikelet form of *P. sciurotoides*: BRAZIL. RIO DE JANEIRO: between Alta Bôa Vista and Silvestre, vicinity of Rio de Janeiro, 450–520 m, 23 Jan. 1925, *Chase 8374* (F, NY, US); camino Dos Macacos, Jardim Botânico to Alta Bôa Vista, vicinity of Rio de Janeiro, 100–200 m, 12 Feb. 1925, *Chase 8446* (US); Corcovado, Sep. 1920, *Kuhlmann & Ducke 16233* (SI); Corcovado, vicinity of Rio de Janeiro, 700 m, 11 Jan. 1925, *Chase 8169* (F, GH, MO, NY); Corcovado, 6 Mar. 1924, *Bailey & Bailey 742* (US); Tijuca, 1,000 m, 28 Apr. 1930, *Chase 12158* (US).

These specimens, included provisionally in *P. sciurotoides*, have spikelets 1.9–2.2 mm long and panicles 3.5–8 cm long. They were collected in Rio de Janeiro, Brazil, in mountains of the Serra do Mar, scandent on the forest margins.

**28. Panicum scoparium** Lam., Encycl. 4: 744. 1798. *Dichanthelium scoparium* (Lam.) Gould, Brittonia 26: 60. 1974. TYPE: United States. South Carolina: without locality, *Michaux s.n.* (holotype, P-MICH; photo and fragment, US 2808935). Figure 28.

Plants perennial with a rosette of winter leaves. *Culms* ascending, slightly decumbent at the base, to erect, to 1.6 m tall, simple and then freely branching at the upper nodes; internodes cylindric, hollow, villous, covered with appressed whitish hairs, purplish to greenish, nodes densely pilose, covered with retrorse whitish hairs, with a glandular zone below. *Sheaths* striate, densely papillose-pilose and covered with conspicuous glands, the margins shortly pilose. *Ligules* membranous-ciliate, 1.5–2.5 mm long, membranous portion inconspicuous or to 0.5 mm long. *Blades* lanceolate, (2–)10–19 cm long, (0.3–)1.5–1.8 cm wide, flat, the base subcordate, the apex attenuate, hispid on both surfaces, the margins shortly pilose, the midnerve conspicuous. *Inflorescences* terminal and axillary from the uppermost nodes, terminal inflorescence exserted, peduncle hispid, ca. 25 cm long; *panicles* lax, open, diffuse, 10–18 cm long; *main axis* flexuous, hispid and covered with conspicuous glands, the branches alternate to opposite, divergent, the

axis of the branches hispid toward the base, otherwise glabrous, glandular; pedicels solitary, 1–15 mm long, glabrous and covered with glands; terminal panicles with chasmogamous flowers; axillary panicles ca. 4 cm long, similar to the terminal one. *Spikelets* solitary, obovoid, 2.5–2.8 mm long, 1.3–1.6 mm wide, greenish to purplish. *Lower glume* truncate to ovate, 0.4–0.8(–1.5) mm long, ⅐–¼ or occasionally slightly longer than ½ the length of the spikelet, nerveless to 1-nerved. *Upper glume and lower lemma* subequal or the upper glume shorter and not covering the upper anthecium, obtuse, 9-nerved. *Lower palea* lanceolate, hyaline, 1.3 mm long, 0.6 mm wide; lower flower absent. *Upper anthecium* ellipsoid, 2–2.2 mm long, 0.9–1.4 mm wide, smooth, shining, pale, glabrous, papillose, shortly apiculate. *Caryopsis* obovoid, 1.5 mm long, 1.2 mm wide, olivaceous and with dark spots; hilum punctiform, embryo less than ½ the length of the caryopsis.

*Distribution and ecology:* southeastern United States, Mexico, and the West Indies, in marshes, moist pinewoods, and roadsides.

*Selected specimens cited.* CUBA. ORIENTE: Chanascal de la Cueva, Sierra de Nipe, *León 19856* (MO); crest of Sierra Nipe, *Morton & Acuña 3082* (US); pine woods, iron mine, S of Guaro, *Hitchcock 23414* (US). DOMINICAN REPUBLIC. Cordillera Central, near La Cumbre, *Ekman 11432* (G, US). LA VEGA: vicinity of Constanza, 1,000–1,600 m, *Allard 17485* (US); 16 km E of El Río along hwy., 1,220 m, *Davidse 2657* (MO); 18 km S of Jarabacoa along the highway, 1,160 m, *Davidse 2651* (MO). MONTE CRISTI: Lagunas de Cenobí, *Ekman 12943* (US). SAN JUAN: Piedra del Aguacate to Río del Oro, *Howard & Howard 9331* (US). SANTIAGO: declives del Pico de Igua, *Jiménez 1236* (US). HAITI. Massif des Matheux, Grand-Bois, *Ekman 5688* (US); Montagnes Noires, Pet. Riv. de l'Artibonite, between Pérodim and Ingram, *Ekman 3431* (US). PUERTO RICO. Sierra de Naguabo, Río Icaca, *Shafer 3481* (US). UNITED STATES. ARKANSAS: Miller County, collected near Texarkana, *A.A. & E. Geller 4236* (P). DISTRICT OF COLUMBIA: Brookland, *Holm s.n.* (P). SOUTH CAROLINA: Orangeburg, moist sandy soil, *Hitchcock s.n., Amer. Gr. Hb. 178* (P). VIRGINIA: Cape Henry, moist sand along bank of ditch, *Chase s.n., Amer. Gr. Hb. 177* (P).

**29. Panicum sphaerocarpon** Elliott, Sketch Bot. S. Carolina 1: 125. 1816. *Dichanthelium sphaerocarpon* (Elliott) Gould, Brittonia 26: 60. 1974. *Panicum dichotomum* L. var. *sphaerocarpon* (Elliott) Alph. Wood, Class-Book Bot., ed. 1861: 786. 1861. *Panicum microcarpon* Muhlenb. var. *sphaerocarpon* (Elliott) Vasey, Grass. U.S.: 12. 1883. TYPE: United States. Georgia: without locality, *Baldwin s.n.* (holotype, CHARL not seen; photo and fragment, US 81121).

Caespitose perennial, with or without a basal rosette of short, broad leaves. *Culms* decumbent and geniculate, branching at the base, to erect, branching at the upper nodes, 15–40(–60) cm tall; internodes short toward the base, compressed, hollow, glabrous; nodes short-pilose or glabrous. *Sheaths* striate, greenish to purplish, shortly ciliate on the margins, glabrous in the rest of the surface. *Ligules* absent or to 0.8 mm long, short-membranous at base, then long-ciliate, or absent; collar brownish, glabrous. *Blades* lanceolate to ovate-lanceolate, 2.5–9 cm long, 0.5–1.5 cm wide, flat, rigid, glabrous, the base subcordate to cordate, the apex acuminate, the margins scabrous, short-ciliate to ciliate toward the base. *Inflorescences* terminal, exserted, peduncles 6–25 cm long, glabrous; *panicles* lax, diffuse to contracted, (2–)5–11 cm long, 3.5–7 cm wide; *main axis* flexuous, glabrous, glandular; first-order branches alternate, divergent or appressed, distant, the axis of the branches smooth, glabrous, glandular; pedicels long, greenish to purplish, glabrous, smooth, glandular; axillary panicles similar to the terminal one. *Spikelets* solitary, obovoid to broadly ellipsoid, 1.1–1.8 mm long, 0.9–1 mm wide, short-hirsute, the upper glume and lower lemma subequal. *Lower glume* broadly ovate, obtuse, 0.2–0.4(–0.9) mm long, ⅕ the length of the spikelet or occasionally to ⅓–½ the length of the spikelet, nerveless or 1(–3)-nerved separated from the upper glume by a short stipe. *Upper glume* 1.3–1.7 mm long, obtuse, shiny on the inner surface, short-hirsute, 7-nerved, the nerves anastomosing toward the base. *Lower lemma* glumiform, 1.2–1.7 m long, 7-nerved, the nerves anastomosing toward the apex. *Lower palea* ovate-lanceolate, 0.6 mm long, 0.3 mm wide, hyaline, the margins sparsely pilose or glabrous, lower flower absent. *Upper anthecium* broadly ellipsoid, 1–1.3 mm long, 0.6–0.9 mm wide, glabrous, smooth, shiny, indurate, papillose with simple papillae; cleistogamous flowers present or absent. *Caryopsis* obovoid, 0.7 mm long, 0.5 mm wide, brownish; hilum punctiform, embryo ⅓ the length of the caryopsis.

*Panicum sphaerocarpon* is a species with a distinctive anatomy. The absence of differentiation between the spongy and palisade mesophyll separates this species from all others in the section. The chlorenchyma cells are also characteristic in that their cytoplasm is centrally concentrated and adaxial air spaces are present (Fig. 15B, D). In addition, the adaxial bulliform cells are in discrete fans consisting of only 3–4 cells.

KEY TO THE VARIETIES

1. Spikelets 1.1–1.4 mm long ..... var. *floridanum*
1. Spikelets 1.4–1.8 mm long ..... var. *sphaerocarpon*

**29a. Panicum sphaerocarpon** var. **sphaerocarpon**

*Panicum inflatum* Scribner & Smith, U.S.D.A. Div. Agrostol. Circ. 16: 5. 1899. *Panicum sphaerocarpon* Elliott var. *inflatum* (Scribner & Smith) A. Hitchc., in A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 253. 1910. TYPE: United States. Mississippi: Harrison County, Biloxi, *Tracy 4622* (holotype, US).

*Panicum vicarium* Fourn., Mex. Pl. 2: 20. 1886. TYPE: Mexico. Veracruz: Córdoba, *Schaffner 285* (holotype, P).

*Panicum auburne* Ashe, North Carolina Agric. Exp. Sta. Bull. 175: 115. 1900. TYPE: United States. Alabama: Lee County, Auburn, 1898, *Earle & Baker 1527* (isotype, NY; fragment, US 2383621).

*Distribution and ecology:* United States, Mexico, Mesoamerica, and northern South America (Colombia and Venezuela). Grows in forest edges, gravelly banks, or in open sites, in partially disturbed areas, between 600 and 2,700 m.

*Selected specimens cited.* BELIZE. BELIZE: 4 km of Hattieville along the western hwy. to Belmopan, 810 m, *Davidse & Brant 32994* (MO, SI). COLOMBIA. CAUCA: de El Estrecho a Balboa, a 18 km de El Estrecho, 1,280 m, *Zuloaga & Londoño 4249** (COL, SI). ANTIOQUIA: Río Negro, 2,110 m, *Archer 240* (US); Santa Elena, 1,500–2,000 m, *Archer 1167* (US). CUNDINAMARCA: Subida a Alto del Tigre, *Zuloaga 4035** (COL, SI). COSTA RICA. CARTAGO: 3 km S of Agua Caliente, 1,400 m, *Pohl & Davidse 11377* (US). HEREDIA: Volcán Barba, Cordillera Central, *Pohl & Davidse 10535* (MO). SAN JOSE: ca. 2 km SE of Tarbaca on road to San Gabriel, 1,600 m, *Pohl & Davidse 11046* (US). ECUADOR. TUNGURAHUA: Baños al Topo, *Acosta-Solís 20832* (US). EL SALVADOR. CHALATENANGO: E slope of Los Esemiles, *Tucker 1056* (P). SANTA ANA: summit of Cerro Monte Cristo, juncture of Salvador, Honduras, and Guatemala, *Pohl 12572* (MO). GUATEMALA. BAJA VERAPAZ: 6 km N of El Chol, *Harmon & Dwyer 3165* (MO). EL QUICHE: NE of Nebaj, *Metzler 6* (MO). SAN MARCOS: Finca Armenia, San Rafael, pie de la Cuesta, *Dwyer 15207* (MO). HONDURAS. EL PARAISO: Monserrat mountain, *Molina & Molina 27489* (MO). INTIBUCA: Cerro San Cristóbal, La Esperanza, *Ordoñez 85* (MO). FRANCISCO MORAZAN: 2.5 km N of Zambrano, on road to San Francisco de Soroguara, *Pohl & Davidse 12131* (MO). OCOTEPEQUE: common in pine forest and rocky hillsides of Machuca, Honduras and Guatemala border, *Molina & Molina 27870* (MO). OLANCHO: Río El Salto, 5 km al W, Campamento, *Amador 89* (MO); Montaña Los Zapotes, 10 km W de Campamento, *Galeano 98* (MO). MEXICO. CHIAPAS: Mun. Teopisca, marsh near Teopisca, *Breedlove & Davidse 54814* (MO); Mun. La Trinitaria, 9 km S of Comitan on Mexican Hwy. 190, *Breedlove & Davidse 54954* (MO). GUERRERO: 3.5 km al N de Zoyotepec, brecha maderera, *Martínez-Salas & Torres 2562* (MO). JALISCO: E of San Sebastián, Hacienda del Ototal, *Mexía 1812* (MO). MICHOACAN: ca. 10 mi. W of Ciudad Hidalgo, near km Post 160 on Hwy. 15 to Morelia, *Davidse & Davidse 9842* (MO). VERACRUZ: Orizaba, *Hitchcock s.n.*, Amer. Gr. Hb. 155 (MO, P); sand bluffs near Jalapa, 4,000 ft., *Pringle 8344* (MO, P). NICARAGUA. ESTELI: along new road from Hwy. 1 (at km 135.5 and ca. 10.6 km W of bridge at La Trinidad) to San Nicolás, *Stevens 14802, 18000* (MO). PANAMA. CHIRIQUI: E slope of Volcán de Chiriquí (Barú), WNW of Boquete, *Davidse & D'Arcy 10153* (MO). VENEZUELA. ARAGUA: Distr. Ricaurte, ca. Colonia Tovar, a 600 m del desvío al Jarillo, vía Colonia Tovar, 2,170 m, *Zuloaga & Ortíz 4280** (MO, SI, VEN). DISTRITO FEDERAL: mountainside between El Junquito and Colonia Tovar, 6,000 ft., *Soderstrom 960* (VEN); ca. 2.5 km down road to Carayaca as measured from intersection with main road between El Junquito and Colonia Tovar, *Davidse & Tillett 4079* (MO).

**29b. Panicum sphaerocarpon** var. **floridanum** Vasey, U.S.D.A. Div. Agrost. Bot. Bull. 8: 33. 1889. *Panicum floridanum* (Vasey) Chapman, Fl. South U.S., ed. 3: 585. 1897, non Trin., 1835. *Panicum erectifolium* Nash, Bull. Torrey Bot. Club 23: 148. 1896. *Dichanthelium erectifolium* (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1105. 1978. *Dichanthelium sphaerocarpon* (Elliott) Gould var. *floridanum* (Vasey) Davidse, Novon 2: 104. 1992. TYPE: United States. Florida: "Moist pine barrens, Mosquito Inlet," May 1879, *Curtiss 3599* (lectotype, US 81122; isolectotype, MO). Figure 29.

*Distribution and ecology:* open white-sand savannas and moist pine woods of southeastern United States, Belize, and Cuba, 0–100 m.

*Additional specimens examined.* BELIZE. BELIZE: 12.5 mi. NW of Belize along Northern Hwy., *Croat 23259* (MO), *Dwyer 10716* (MO); savanna near Ridge Lagoon Plantation, 11 mi. from Belize on Northern Hwy., *Gentry 7860* (MO). CUBA. ISLA DE LA JUVENTUD: about 5 km S of Santa Bárbara, *Blanco s.n.* (US 2183813), *Killip 44825* (US); along road to San Francisco de las Piedras, *Killip 43723, 44193* (US). ORIENTE: Moa, champ d'aviation, *Victorin et al. 21448* (US). PINAR DEL RIO: Herradura, at a small laguna, *Ekman 11599* (US); La Grifa, in open places, *Ekman 11242* (US); between Guane and Remates, near sea level, edge of Laguna de Cebo, *Killip 32328a* (US). SANTA CLARA: Motembo, *León et al. 8615* (US).

Variety *floridanum* differs from variety *sphaerocarpon* by its smaller spikelets 1–1.5 mm long, erect leaves that are appressed to the culms, glabrous nodes, and ligules 0.3–0.4 mm long.

**30. Panicum stigmosum** Trin., Gram. Panic. 194. 1826. TYPE: Brazil. Minas Gerais: "ad rip. rivuli Pibanha, in Serra dos Orgaos, l. mis. mense Aprili *Riedel*" (holotype, LE not seen; photo of the type, K, fragment, US 974621). Figures 16, 29.

*P. mollicomum* Kunth, Revis. Gramin. 1: Suppl. 9. 1830. *P. lanuginosum* J. S. Presl, Reliq. Haenk. 1: 306. 1830, non Elliott, 1816. TYPE: "Peru," without locality, *Haenke s.n.* (PR, holotype not seen; fragment of the type, US 974627).

Perennial, (30–)50–100 cm tall. *Culms* decumbent, branching and rooting at the lower nodes, then ascendent, leaning on vegetation, branching at the upper nodes; internodes 4–19 cm long, compressed, glabrous, with glands toward the distal portion; nodes compressed, brownish, pilose or glabrous. *Sheaths* 3–11 cm long, shorter than the internodes, hispid or glabrous, glandular, one margin ciliate, the other one ciliate toward the apex but otherwise glabrous. *Ligules* (0.3–)1–1.6 mm long, shortly membranous at the base, then ciliate; collar villous or puberulous, brownish. *Blades* linear-lanceolate, 10–22 cm long, 1–2.2 cm wide, the base subcordate or cordate, slightly asymmetrical, the apex attenuate, sparsely pilose or glabrous on the adaxial surface or hispid on both surfaces, the margins shortly ciliate, scabrous, the abaxial surface glandular or eglandular. *Inflorescences* exserted, peduncle (6–)9–34 cm long, cylindric, glabrous or sparsely pilose, glandular; panicles lax, diffuse, 9–21 cm long, 6–15 cm wide; *main axis* flexuous, glabrous or sparsely pilose, glandular, the pulvini pilose, first-order branches divergent, alternate or subopposite, flexuous, the axis of the branches flexuous, scaberulous, glandular; pedicels claviform, shortly hirsute or scabrous. *Spikelets* ellipsoid or obovoid, (1.9–)2.4–3.2 mm long, (0.9–)1.1–1.3 mm wide, greenish to purplish, glabrous, shortly stipitate, the upper glume and lower lemma subequal. *Lower glume* ovate, 1.1–1.8 mm long, ½–¾ the length of the spikelet, embracing the upper glume, (1–)3-nerved, glabrous. *Upper glume* (1.6–)2–2.4 mm long, not covering the apex of the upper anthecium, glabrous, 7–9-nerved, the nerves manifest. *Lower lemma* glumiform, (1.6–)2–2.4 mm long, 7–9-nerved. *Lower palea* lanceolate, (1.6–)1.8–2.1 mm long, 0.6–0.7 mm wide, hyaline, glabrous, the margins ciliate; lower flower present or absent, male when present; stamens 3, anthers to 0.9 mm long. *Upper anthecium* ellipsoid, 1.9–2.1 mm long, 0.9–1 mm wide, acuminate, stramineous, indurate, with simple papillae all over its surface; lodicules ca. 0.3 mm long; stamens 3, the anthers 0.7 mm long. *Caryopsis* ellipsoid, 1.3 mm long, 1 mm wide; hilum punctiform, embryo ⅓ the length of the caryopsis.

*Distribution and ecology:* Brazil, in the states of Espírito Santo, Minas Gerais, Rio de Janeiro, Santa Catarina, and São Paulo, on forest edges in tangled colonies, 1,000–2,200 m.

*Additional specimens examined.* BRAZIL. ESPIRITO SANTO: Serra do Caparaó, *Chase 10106*, *10112* (US). MINAS GERAIS: Parque Nac. Itatiaia, camino para las Agulhas Negras, *Zuloaga et al. 2382* (RB, SI, US); Serra da Gramma, 1,100 m, *Chase 9543* (US), 1,700 m, *Chase 9556* (NY); Serra do Caparaó, 2,100–2,200 m, *Chase 9662* (F, NY, US); Itacolumí, E of Ouro Preto, *Chase 9381* (NY, US), *9421* (US). RIO DE JANEIRO: Floresta Regime de Preservaçao Permanente do IBDF, entre Vale dos Princesas y Rocio, 1,000–1,200 m, *Zuloaga et al. 2389* (SI); Macieiras, Serra de Itatiaia, *Chase 8261* (F, NY, US), *8322* (US), *Zuloaga et al. 2351**, *2358** (SI), Rio Campo Belo, *Zuloaga et al. 2363* (RB, SI); Petrópolis, Rio Itamaraby, *Glaziou 17946* (US, W); below Macieiras, Serra de Itatiaia, 1,200–1,800 m, *Chase 8322* (US); Rio de Janeiro, *Glaziou 18629* (US, W). SANTA CATARINA: 41 km S of Campo Alegre, on the road to Jaraguá do Sul, *Smith & Klein 7334* (US). SÃO PAULO: Salesópolis, Estaçao Biológica de Boracéia, *Mattos & Mattos 14248* (P, US). Without state and locality, *Riedel 226* (G).

*Panicum stigmosum* is closely related and perhaps conspecific with *P. sabulorum*, differing only in: the plants being bigger, scandent; foliar dimorphism is absent; the inflorescence is bigger ((6–)9–34 cm long); and leaf blades and axis of the inflorescence are glandular. There are several intermediate specimens between both species, however, such as *Zuloaga et al. 2351*, *2382*, *Glaziou 17946*, *18629*, *Chase 9361*, *9381*, *9421*, and *Mattos & Mattos 14248*.

Macrohairs are lacking in the two specimens examined in the anatomical study (Fig. 16D, E). The mesophyll is characteristically very diffuse with large intercellular air spaces.

*Panicum stigmosum* var. *parviflorum* Doell is a dubious name. Doell included in his original diagnosis two specimens: *Sellow 4906* and *Regnell III-1360*. There is a fragment of the latter specimen at US which is *P. pantrichum* Hackel (sect. *Cordovensia*).

Small-spikelet form of *P. stigmosum*: BRAZIL. ESPIRITO SANTO: Serra do Caparaó, *Chase 10105* (MO, US). MINAS GERAIS: Serra da Gramma, E of Araponga, 1,200 m, *Chase 9531* (F, GH, MO, NY, US). RIO DE JANEIRO: Serra de Itatiaia, Macieiras, 1,700–1,800 m, *Chase 8321* (GH, NY, US).

These specimens have spikelets 1.9–2.1 mm long, but are otherwise similar in all characters to other material *P. stigmosum*. The rachilla is prolonged as a short mucro above the upper anthecium in *Chase 10105*.

**31. Panicum stipiflorum** Renvoize, Kew Bull. 37: 329. 1982. TYPE: Brazil. Bahia: 16 km NW of Lagoinha, which is 5.5 km SW of Delfino on side road to Minas do Mimoso, 950–1,000 m, 8 Mar. 1974, *Harley, Renvoize, Erskine, Brighton & Pinheiro 17019* (holotype, CEPEC; isotypes, K, NY, US 2955108). Figure 29.

Annual? *Culms* decumbent at the base, then ascendent, 20–30(–80) cm tall, freely branching at the upper nodes, many-noded, internodes terete, hollow, short-pilose, nodes compressed, densely pilose with short, appressed, whitish hairs. *Sheaths* striate, sparsely or densely hirsute with short hairs, or long-pilose in the upper portion, the margins long-ciliate, more so in the upper portion. *Ligules* 0.3 mm long, membranous-ciliate. *Blades* ovate-lanceolate, 2–6 cm long, 0.6–1.5 cm wide, cordate, amplexicaulous, sparsely to densely hirsute with short, rigid hairs, or glabrescent, the margins cartilaginous, scabrous and long-ciliate with papillose-pilose hairs. *Inflorescences* terminal, exserted, peduncles to 20 cm long, cylindric, shortly hirsute; *panicles* lax, diffuse, 3–8 cm long, 2–5 cm wide; *main axis* flexuous, hirsute; pulvini densely pilose; first-order branches alternate, divergent, the axis of the branches hirsute, smooth, eglandular; pedicels hirsute, 0.6–2 mm long. *Spikelets* paired or solitary, ellipsoid, 2.2–2.6 mm long, 0.9 mm wide, sparsely hirsute with short hairs on the glumes and lower lemma, greenish or tinged with purple. *Lower glume* acute, ½ or less the length of the spikelet, occasionally larger, not embracing the upper glume at its base, 3–5-nerved, separated from the upper glume by a conspicuous stipe. *Upper glume* 1.8–2.1 mm long, occasionally a little smaller and not covering the apex of the upper anthecium, 7–9-nerved, the nerves anastomosing. *Lower lemma* glumiform, 7-nerved, the nerves anastomosing toward the apex. *Lower palea* elliptical, 1.5 mm long, 0.3 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 1.7–1.8 mm long, 0.7 mm wide, indurate, smooth, shiny, papillose with simple papillae regularly distributed all over its entire surface; lemma 5-nerved, shortly apiculate and pilose toward the apex. *Caryopsis* ellipsoid, 1.5 mm long, 0.9 mm wide; hilum punctiform, embryo ⅓ the length of the caryopsis.

*Distribution and ecology:* Bahia, Brazil, in cerrados in rocky, sandy soils, between 900 and 1,100 m, in flower between February and April.

*Additional specimens examined.* BRAZIL. BAHIA: 34 km E of Morro do Chapéu along Hwy. BA-052, Chapada da Diamantina, *Davidse et al. 11888* (K, MO, NY, SI, SP); Chapada da Diamantina, along waterfall of the Rio Ferro Doudo, ca. 21 km E of morro do Chapéu, *Davidse et al. 11950* (MO, SP); 16 km NW of Lagoinha on side road to Minas de Mimoso, 950–1,000 m, *Harley et al. 17004* (paratypes, K, NY, US); Fazenda Mundo Novo, Botafogo, *Zehntner 248, 263* (RB); Serra do Tombador, ca. 18 km E of Morro de Chapéu, *Irwin et al. 30702* (MO, UB); Serra Tinguá, *Zehntner 2017* (M); Sentacé, *Zehntner 2048* (M).

*Panicum stipiflorum* is characterized by its cordate, amplexicaulous leaves with conspicuous ciliate margins, spikelets with a stipe between the lower and upper glume, and lower glume usually less than ½ the length of the spikelet.

**32. Panicum strigosum** Muhlenb. in Elliott, Sketch Bot. S. Carolina 1: 126. 1816. *Dichanthelium strigosum* (Muhlenb.) Freckmann, Brittonia 33: 457. 1981. TYPE: United States. "Hab. in humidis. Car: & Georg:," *Elliott Herb. s.n.* (lectotype, CHARL not seen; isolectotype, US; photo and fragment, US 2808953). Figure 29.

*Panicum ciliatum* Elliott, Sketch Bot. S. Carolina 1: 126. 1816, non *Panicum ciliatum* Maercklin, 1792.

*Panicum dichotomum* L. var. *glabrescens* Griseb., Fl. Brit. W.I. 553. 1864. *Dichanthelium leucoblepharis* (Trin.) Gould & Clark var. *glabrescens* (Griseb.) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1100. 1978. *Dichanthelium strigosum* (Muhlenb.) Freckmann var. *glabrescens* (Griseb.) Freckmann, Brittonia 33: 457. 1981. TYPE: Jamaica. Without locality, *Purdie s.n.* (holotype, K).

*Panicum laxiflorum* Lam. var. *pubescens* Vasey, Contr. U.S. Natl. Herb. 3: 30. 1892. *Dichanthelium leucoblepharis* (Trin.) Gould & Clark var. *pubescens* (Vasey) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1101. 1978. *Panicum ciliatum* Elliott var. *pubescens* (Vasey) Freckmann ex R. W. Pohl, Fieldiana, Bot., n.s. 4: 356. 1980. *Panicum leucoblepharis* Trin. var. *pubescens* (Vasey) Beetle, Phytologia 48: 192. 1981. TYPE: United States. Florida: Duval County, without locality, *Curtiss s.n.* (lectotype, US).

*P. polycaulon* Nash, Bull. Torrey Bot. Club 24: 200. 1897. TYPE: United States. Florida: Hillsborough County, Tampa, 20 Aug. 1895, *Nash 2420a* (holotype, NY; isotype, US).

*P. longipedunculatum* Scribner, Tennessee Agric. Exp. Sta. Bull. 7: 53. 1894. TYPE: United States. Tennessee: White Cliff Springs, July 1890, *Scribner s.n.* (lectotype, US 742594).

Short-rhizomatous perennials, caespitose and with many fasciculate culms. *Culms* erect, 3–20 cm tall, few-noded, unbranched below the inflorescence; internodes short, cylindric, hollow, short-pilose or glabrous; nodes pilose, compressed. *Sheaths* 1 cm long, longer than the internodes, striate, glabrous, one margin ciliate, the other membranous. *Ligules* 0.2–0.4 mm long, membranous-ciliate; collar glabrous. *Blades* lanceolate, 1–5(–7) cm long, 0.3–0.5(–0.7) cm wide, flat, glabrous or with long sparse hairs, the base narrowed or subcordate, the apex acute, the margins long-ciliate with rigid papillose-pilose hairs or occasionally glabrous. *Inflorescences* terminal, exserted, peduncle 1–14 cm long, flexuous, glabrous or sometimes hirsute near the junction with the panicle; *panicles* lax, diffuse, few-flowered, 2–5 cm

long, 1.5–4.5 cm wide; *main axis* flexuous, densely hirsute with long whitish hairs, occasionally glabrous, glandular, the pulvini pilose; first-order branches alternate, the axis of the branches hirsute, flexuous and glandular; pedicels glabrous, claviform, glandular; axillary inflorescences present, similar to the terminal one. *Spikelets* solitary, obovoid or ellipsoid, 1–1.7 mm long, 0.6–0.9 mm wide, puberulous or glabrous, greenish to purplish, the upper glume and lower lemma subequal. *Lower glume* ovate, 0.5–0.8 mm long, ⅓–⅔ the length of the spikelet, nerveless or 1-nerved, embracing the upper glume at its base, acute or truncate, with a small internode between the lower and upper glume. *Upper glume* obtuse, 7-nerved. *Lower lemma* 7-nerved, glumiform, obtuse. *Lower palea* 0.3–0.7 mm long, 0.1–0.2 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ovoid, 1–1.2 mm long, 0.6–0.9 mm wide, biconvex, whitish, indurate, smooth, glabrous, papillose; lemma shortly apiculate; stamens 3, the anthers 0.5 mm long. *Caryopsis* unknown.

*Distribution and ecology:* southern United States, Mexico, Mesoamerica, and the West Indies, in South America in Colombia and Venezuela. Commonly found in wet meadows or swampy areas and savannas, between sea level and 2,100 m.

*Selected specimens cited.* BELIZE. BELIZE: 4 km W of Hattieville along the western hwy. to Belmopan, 80 m, *Davidse & Brant 32982* (MO, SI). EL CAYO: Mountain Pine Ridge, along Coona Cairn Road, *Davidse & Brant 33037A* (MO). ORANGE WALK: savanna ca. 5 km N of August Pine Ridge on the road to Trinidad, *Davidse & Brant 32810* (MO). STANN CREEK: in pine ridge, Mullins River Pine Ridge, *Gentle 8550* (NY). TOLEDO: Swasey Branch, Monkey River, *Gentle 3748* (MO). COLOMBIA. CAUCA: Cuatro Esquinas, 1,700–1,800 m, *Pennell & Killip 6362* (NY, US); Munchique, 2,100 m, *Alston 8205* (COL, US). MAGDALENA: Santa Marta, *Smith 163* (MO, NY, P, US). COSTA RICA. GUANACASTE: región del Volcán Cacao, Cerro Pelado, *Chacon 2266* (MO). CUBA. ISLA DE LA JUVENTUD: near Nueva Gerona, *Palmer & Riley 990* (US); between San Francisco de Las Piedras and Cerro La Cañada, moist soil along stream, *Killip 44614* (US). ORIENTE: Sierra de Nipe, in pineland savannas at foot of Loma Mensura, 725 m, *Ekman 9704* (US). PINAR DEL RIO: NW of Pinar del Río, *Hitchcock 23299* (US); Mántua, *Ekman 11088* (G); Sierra de los Organos, Grupo del Rosario, Pinar de Lechuza, *Ekman 12969* (G, NY, US). DOMINICAN REPUBLIC. Llano costero, Cuenca, *Ekman 11068* (G, US); sabana de Santa Rosa, 190 m, *Allard 15870* (US). GUATEMALA. ALTA VERAPAZ: vicinity of Secanquim, 550 m, *Pittier 257* (US). PETEN: Tikal National Park, Bajo de Santa Fé, in pinal, *Contreras 528* (US). HAITI. Massif du Nord, Marmelade, *Ekman 8206* (G, US). HONDURAS. GRACIAS A DIOS: Tuas, campamento maderero al W de Brus Laguna, *Nelson & Hernández 1005* (MO). OLANCHO: Vaguada del Río de la población de Culmi, *Nelson & Romero 4708* (MO). JAMAICA. Halliss Savanna, Upper Clarendon, *Harris 12225* (MO, US); James Hills, Savanna, *Harris 12852* (MO, US); Bull Head Mountain and vicinity, *Hitchcock 9550, 9551* (US). MEXICO. CHIAPAS: Municipio of Palenque, 8–12 km N of Palenque on road to Catazaja, *Breedlove 55356* (MO). NICARAGUA. ZELAYA: ca. 3 km S of Bilwaskarma, *Pohl & Davidse 12262* (MO); along Río Tuapi from bridge (on road between Puerto Cabezas and Tuapi) to coast, *Stevens 7816* (MO). PANAMA. BOCAS DEL TORO: Santa Catalina, *Blackwell et al. 2696* (MO). COCLE: Caribbean side of divide at El Copé, *Hamilton & Davidse 2634* (MO). HERRERA: 10 km W of Las Minas on road to El Toro, roadside and cafetal, *Sytsma & D'Arcy 3221* (MO). PANAMA: Distrito Capira, Cerro Campana, *van der Werff & Herrera 6167* (MO); hills NE of Hacienda La Joya, *Dodge et al. 16884* (MO). VERAGUAS: along beach, Concepción, *Hammel 5237* (MO). PUERTO RICO. Monte Mesa, vicinity of Mayagüez, *Chase 6276* (US); Campo Alegre, between Manatí and Laguna del Tortuguero, *Chase 6621* (US).

**33. Panicum superatum** Hackel, Oesterr. Bot. Z. 51: 427. 1901. TYPE: Brazil. Rio de Janeiro: Serra dos Orgãos, 7 Mar. 1889, *Glaziou 17904* (holotype, W; isotype, P, fragment, P, fragments US 1280065, 1715312). Figures 17, 31, 35.

Caespitose, short-rhizomatous perennial. *Culms* erect to ascendent, (0.1–)0.2–1.2 m tall, branching at the base or from the upper nodes; internodes 4–6 cm long, hispid or glabrous, terete, hollow; nodes compressed, long-pilose, or glabrous. *Sheaths* 4–10 cm long, striate, glabrous or hirsute with long papillose-pilose hairs, one margin long-ciliate, the other membranous. *Ligules* membranous-ciliate, 0.6–1.5 mm long; collar glabrous or densely pilose. *Blades* lanceolate to linear-lanceolate, 4.5–16 cm long, 0.6–1.5(–2.5) cm wide, hispid or glabrous, densely pilose on the adaxial surface near the subcordate or cordate base, the apex attenuate, the margins ciliate. *Inflorescence* terminal, exserted, peduncle hispid; *panicles* contracted to slightly open, 5–8(–17) cm long, 0.8–5(–10) cm wide; *main axis* hispid, the pulvini pilose; first-order branches appressed or slightly divergent from the main axis, alternate or subopposite, the axis of the branches hispid or short-pubescent and eglandular; pedicels flexuous, scabrous, hispid with long hairs. *Spikelets* congested, obovoid, (2.1–)2.4–3.3 mm long, 0.9–1.2 mm wide, sparsely pilose or glabrous, the upper glume and lower lemma subequal, shortly stipitate. *Lower glume* ovate-lanceolate, 1.6–2.4 mm long, ½–¾ the length of the spikelet, clasping, 3–5-nerved, with a short stipe between the lower and upper glume. *Upper glume* (1.8–)2.4–2.5 mm long, (7–)9–11-nerved, not covering the apex of the upper anthecium. *Lower lemma* (1.9–)2.2–2.5 mm long, 7–9-nerved. *Low-*

FIGURE 35. *Panicum superatum.*—A. Habit.—B. Spikelet, lower glume view.—C. Spikelet, upper glume view.—D. Spikelet, lateral view.—E. Lower palea.—F. Upper anthecium, lemma view.—G. Upper anthecium, palea view.—H. Detail of apex of the lemma.—I. Caryopsis, embryo view.—J. Caryopsis, hilum view. (All based on *Chase 9350.*)

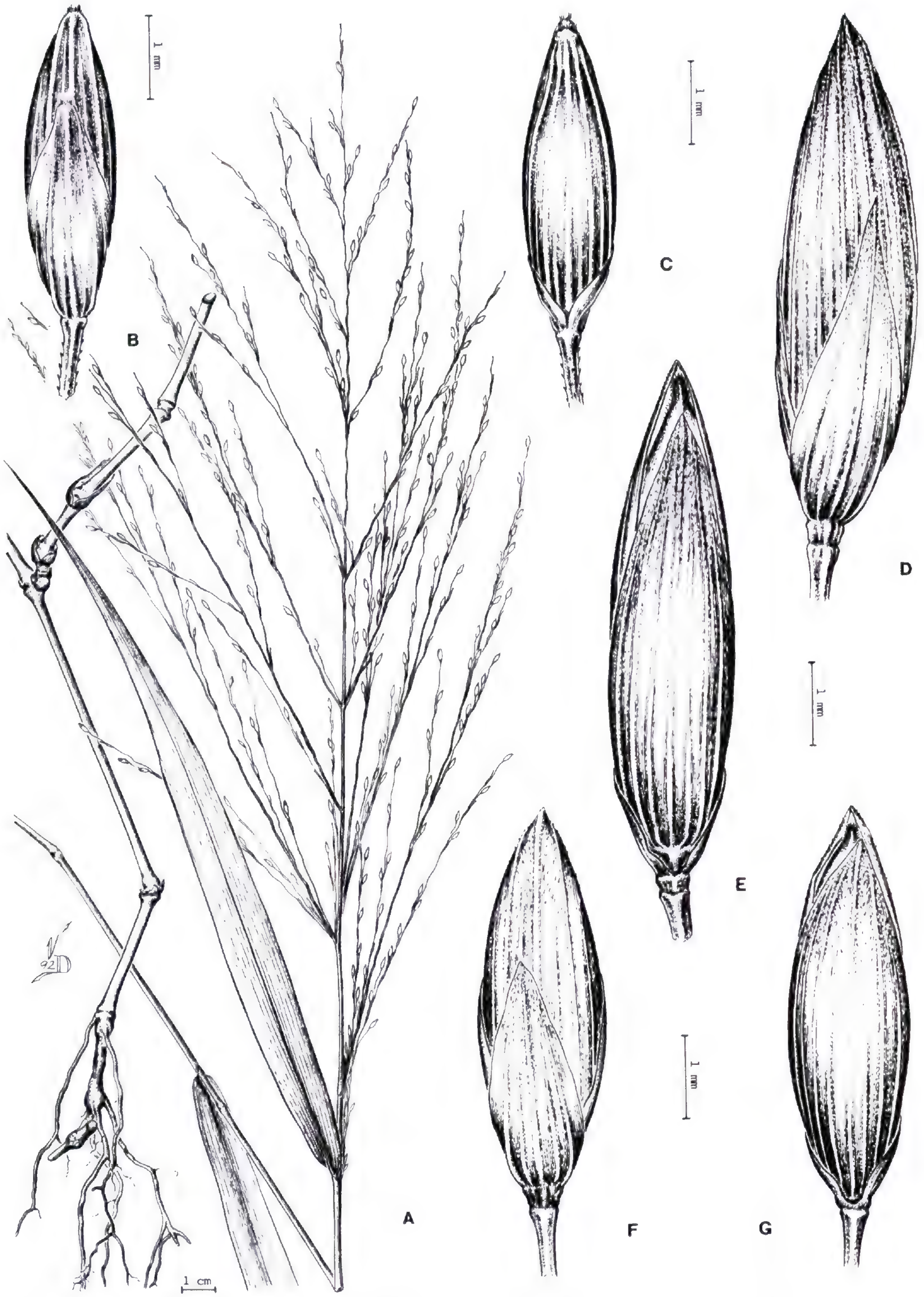


FIGURE 36. A–C. *Panicum penicillatum.* — A. Habit. B. Spikelet, lower glume view. — C. Spikelet, upper glume view. D, E. *Panicum caparaoense.* D. Spikelet, lower glume view. — E. Spikelet, upper glume view. F, G. *Panicum itatiaiae.* — F. Spikelet, lower glume view. — G. Spikelet, upper glume view. (A–C, based on *Alvarenga & Oliveira 525*; D, E, based on *Hatschbach & Guimaraes 45170*; F, G, based on *Chase 8327.*)

*er palea* lanceolate, (1.5–)2.1 mm long, 0.6 mm wide, membranous, the margins ciliate; lower flower absent or present, male when present, with 3 anthers each 1 mm long. *Upper anthecium* ellipsoid, 1.9–2.5 mm long, 0.9–1.2 mm wide, indurate, smooth, the apex of the lemma apiculate, scaberulous; stamens 3, the anthers 0.3–1 mm long. *Caryopsis* ellipsoid, 1.7 mm long, 1 mm wide; hilum punctiform, embryo ⅓ the length of the caryopsis.

*Distribution and ecology:* Brazil, on mountain slopes from Espírito Santo to Rio Grande do Sul, 900–2,650 m.

*Additional specimens examined.* BRAZIL. ESPIRITO SANTO: Serra do Caparaó, rocky open campo, 2,650 m, *Mexía 4014* (NY, P, US); Serra do Caparaó, 2,280–2,400 m, *Chase 10084* (IAN, RB, US). MINAS GERAIS: Barbacena, Serra Mantiqueira, *Chase 8667* (F, US); Ouro Preto, Villa Rica, 1,100 m, *Chase 9350* (F, GH, MO, NY, US); cerrado on middle slopes of Pico de Itacolumí, ca. 3 km S of Ouro Preto, 1,750 m, *Irwin et al. 29483* (MO, UB); Mun. Itamonte, Parque Nacional de Itatiaia, camino para las Agulhas Negras, 1,550–1,800 m, *Zuloaga et al. 2374** (MO, RB, SI, US). PARANA: 4 km E of Guarapuava along highway BR-277 to Curitiba, 1,050 m, *Davidse et al. 11319* (MO); Bocaiuva do Sul, *Clayton 4285* (K). RIO DE JANEIRO: Alto de Itatiaia, 2,200–2,400 m, *Chase 8299* (NY, US, W); Teresópolis, Posse, morro das Antenas de Televisao, *Sucre 2317* (SI); Tijuca, in open spot at summit, *Chase 12161* (US). RIO GRANDE DO SUL: Cambará do Sul-Itaimbezinho-Bela Vista, *Valls et al. 1870, 2903* (CEN); Serra da Rocinha, prope Bom Jesus, in dumetosis, *Rambo 53841* (US). SANTA CATARINA: Mun. Caçador, 9 km W of Caçador, *Smith & Klein 10899* (NY, US); Mun. Bom Jardim da Serra, Alto, 20 km S of Bom Jardim, *Smith & Klein 15809* (HB, NY, P, US); 5 km S of Ponte Alta along highway BR-116 to Lajes, *Davidse et al. 11104* (MO, SP); Ponte Serrado, 94 km W of Joaçaba, 700–900 m, *Smith & Klein 14008* (HB, K, SI); Mun. Urubici, 19 km N of Perico, *Smith & Klein 15889* (HB, US); Mun. Lajes, Serra do Ilhéos, *Smith & Klein 15456* (K, US). SÃO PAULO: Jardin Botânico e Parque do Estado, *Sendulsky 1063* (SI); Campos do Jordão, Serra Mantiqueira, sandy campo, 1,600 m, *Chase 9822* (NY, US).

Related to *Panicum sabulorum* and *P. stigmosum*, *P. superatum* can be distinguished by its contracted panicles and appressed spikelets.

There are two indurate florets in *Chase 9403*. *Sendulsky 1063* has anthers only 0.3 mm long.

**34. Panicum surrectum** Chase ex Zuloaga & Morrone, Novon 1: 111. 1991. TYPE: Brazil. Minas Gerais: Barbacena, long and tangled in moist brushy base of higher slope, *Chase 8664* (holotype, US; isotypes, F, NY). Figures 24D, 30.

Short-rhizomatous perennial. *Culms* decumbent to geniculate, then erect, branching at the upper nodes, scandent, 45–120 cm tall; internodes compressed or cylindric, 7–13 cm long, glabrous; nodes compressed, glabrous, brownish. *Sheaths* 4–10.5 cm long, shorter than the internodes, glabrous to papillose-pilose toward the base, shiny, one margin ciliate, the other one ciliate toward the base, otherwise glabrous. *Ligules* 0.2 mm long, membranous-ciliate; collar pilose. *Blades* linear-lanceolate, 5–12 cm long, 0.6–1 cm wide, glabrous to short-hispid, attenuate at the base and apex, the margins scabrous, long-ciliate toward the base; midnerve conspicuous. *Inflorescences* terminal, exserted; *panicles* lax, diffuse, 3.5–15 cm long, 3–10 cm wide; *main axis* glandular or eglandular, flexuous, glabrous, the pulvini glabrous; first-order branches ascendent, whorled toward the base, then subopposite or alternate, the axis of the branches glabrous, flexuous, glandular or eglandular; pedicels triquetrous, glabrous, glandular or eglandular. *Spikelets* narrowly ellipsoid, 1.8–2.2 mm long, 0.8 mm wide, glabrous, greenish, nonstipitate, the upper glume and lower lemma subequal, the nerves manifest. *Lower glume* ovate, 0.9–1.3 mm long, ⅖–½(–¾) the length of the spikelet, not embracing the upper glume, (1–)3-nerved, the lateral nerves inconspicuous. *Upper glume* 1.6–2 mm long, not covering the apex of the upper anthecium, 9-nerved. *Lower lemma* glumiform, 1.8–2.1 mm long, 9-nerved. *Lower palea* lanceolate, 1.5–1.8 mm long, 0.4 mm wide, shortly pilose near the apex, otherwise glabrous, hyaline; lower flower male or sterile, stamens 3, the anthers 1 mm long. *Upper anthecium* ellipsoid, 1.6–1.8 mm long, 0.7 mm wide, pale, indurate, papillose, the apex of the lemma shortly crested and pilose; stamens 3, the anthers 1.2 mm long, purplish. *Caryopsis* ovoid, 1.3 mm long, 0.7 mm wide; hilum punctiform, embryo less than ¾ the length of the caryopsis.

*Distribution and ecology:* Brazil, occasionally present in Paraguay, found at forest edges, between 600 and 1,800 m.

*Additional specimens examined.* BRAZIL. DISTRITO FEDERAL: ca. 35 km E of Brasília, *Irwin & Soderstrom 5419* (NY, UB, US). GOIAS: Luziania, 15 km ao S da cidade, *Heringer 18124* (IBGE, RB). MATO GROSSO DO SUL: Dourados, *Chase 11023* (IAN). MINAS GERAIS: 19 km NE of the intersection of Hwys. 381 and 459, ca. 12 km SW of São Gonçalo do Sapucai, 870 m, *Davidse & Ramamoorthy 10602* (MO, SI); Itacolumy, E of Ouro Preto, 1,400 m, *Chase 9380* (NY, US), *9407* (US); Juiz de Forá, *Krieger SVD 1227* (RB, US); Poços de Caldas, 1,100–1,500 m, *Chase 10677* (NY, SP, US); Serra da Gramma, 1,700 m, slope above jungle, *Chase 9555* (F, GH, NY, US). PARANA: Mun. Gral. Carneiro, Rio Lageado, *Hatschbach et al. 13731* (K); Três Barras, *Dusén 17531* (F, G, GH, NY, US). RIO DE JANEIRO: below Macieiras, Serra de Itatiaia, 1,700–1,800 m, *Chase 8324* (GH, NY,

US). RIO GRANDE DO SUL: Taimbezinho, pântano, *Boechat s.n.* (ICN 41067). SANTA CATARINA: Rio Capinzal, *Dusén 17876* (US); Santa Cecilia, 1,100 m, *Reitz & Klein 11358* (US). SÃO PAULO: Serra Mantiqueira, Campos do Jordao, 1,580 m, open sandy campo, *Chase 9815* (F, NY, US) *9839* (NY, US), *Holway 1737* (US), *Leite 3510* (GH). PARAGUAY. CAAGUAZU: Caaguazú, *Balansa 7* (G).

*Panicum surrectum* shows affinities with *P. sabulorum*, *P. stigmosum*, and *P. superatum*. *Panicum surrectum* is characterized by its long-ellipsoid spikelets, and smaller lower glume, not embracing the upper glume. *Panicum stigmosum*, *P. sabulorum*, and *P. superatum* have a lower glume ½–¾ the length of the spikelet, covering the base of the upper glume, and ellipsoid to obovoid, globose spikelets. Additionally, in *P. superatum* the panicles are contracted, with the spikelets congested on the branches, and *P. stigmosum* has bigger spikelets, (2–)2.4–3.2 mm long, and leaves 10–22 cm long.

*Panicum surrectum* has, as other species of subgenus *Dichanthelium* (Morrone & Zuloaga, 1991), conspicuous glands on the axis and pedicels of some specimens.

Cleistogamous flowers were observed in *Chase 9815*, with anthers 0.6 mm long.

**35. Panicum telmatum** Swallen, Phytologia 14: 81. 1966. TYPE: Frontier between Roraima, Brazil and Bolívar, Venezuela, Serra do Sol, 28 Dec. 1954, 2,100 m, *Maguire & Maguire 40400* (holotype, US 2182190; isotype, NY). Figure 31.

Tufted perennial. *Culms* elongated, arching, branching, internodes cylindric, hollow, densely hispid with appressed hairs; nodes pilose. *Sheaths* papillose-pilose to short-pilose, the margins long-ciliate. *Ligules* membranous-ciliate, membranous portion 0.2 mm long, cilia 0.8–1 mm long, collar pilose with whitish hairs. *Blades* lanceolate, 3.5–5.5 cm long, 4–9 mm wide, flat, the base rounded, the apex acuminate, the adaxial surface sparingly hispid and with long, whitish hairs near the ligule, the abaxial surface scabrous, the margins long-ciliate. *Inflorescence* with base included in uppermost sheath or short-exserted, 3–5 cm long, pyramidal, few-branched, the branches divergent from the axis; *main axis*, the branches and pedicels hirsute with whitish hairs. *Spikelets* solitary, ellipsoid, 3–3.2 mm long, 1.2–1.4 mm wide, minutely appressed-puberulent; lower glume separated from the upper glume by a short internode. *Lower glume* 2–2.3 mm long, broadly ovate, blunt, 3–5-nerved, about ¾ the length of the spikelet, the nerves anastomosing. *Upper glume and lower lemma* as long as spikelet, broadly rounded on back, 7–9-nerved, the nerves anastomosing toward the apex. *Lower palea* ovate, 2 mm long, 0.6–0.8 mm wide, ca. ⅔ as long as the lemma, hyaline, glabrous, the margins short-ciliate, the lower flower absent. *Upper anthecium* ellipsoid, 2.3–2.5 mm long, 1.1 mm wide, nearly as long as spikelet, glabrous, short-pilose at the apex of the lemma; lemma 7-nerved, with simple papillae over its entire surface. *Caryopsis* unknown.

*Distribution and ecology:* endemic to Uei-tepui (Cerro del Sol), Venezuela, about 25 km SE of Mt. Roraima, where growing in "burnt part of boggy central area."

*Additional specimens examined.* VENEZUELA. BOLIVAR: Distr. Roscío, altiplanicie que rodea la cumbre del Uei-tepui (Cerro del Sol), sector occidental por encima del valle del Río Arabopo, *Huber 10008* (MO, MYF, SI).

*Panicum telmatum* is related to *P. sabulorum*; the latter species has smaller, biconvex obovoid spikelets 1.9–3 mm long and is known from central and southern Brazil, Paraguay, Uruguay, Bolivia, Chile, and Argentina.

**36. Panicum umbonulatum** Swallen, Contr. U.S. Natl. Herb. 29: 420. 1950. *Dichanthelium umbonulatum* (Swallen) Davidse, Novon 2: 105. 1992. TYPE: Guatemala. Zacapa: upper slopes of Sierra de Las Minas, along Río Repollal, 2,100–2,400 m, 12–13 Jan. 1942, *Steyermark 42469* (holotype, US 1935002; isotypes, F, NY). Figure 31.

*Panicum alcobense* Swallen, Contr. U.S. Natl. Herb. 29: 423. 1950. TYPE: Guatemala. Jalapa: collected in oak wood around top of Cerro Alcoba, just E of Jalapa, 1,700 m, 2 Dec. 1939, *Steyermark 32515* (holotype, F 1040005; fragment and photo, US 2236474).

*Panicum ramiparum* Swallen, Contr. U.S. Natl. Herb. 29: 423. 1950. TYPE: Guatemala. Quezaltenango: collected in mountains near Santa María, S of Quezaltenango, 25 Mar. 1932, *Weatherwax 160* (holotype, US 1914983).

Perennial without a basal rosette of broader leaves. *Culms* decumbent, rooting and branching at the lower nodes and trailing, to erect, 40–100 cm tall, internodes terete, hispid, greenish to purplish; nodes compressed, purplish, densely papillose-pilose with whitish retrorse hairs. *Sheaths* striate, papillose-pilose with deciduous tuberculate hairs, the margins ciliate. *Ligules* membranous-ciliate, 0.6–1 mm long; pseudoligule present, with long hairs at the adaxial surface of the blade; collar

densely pilose. *Blades* lanceolate, 5–12 cm long, 0.4–1.4 cm wide, flat, the base cordate to subcordate, the apex acuminate, short-hispid on the adaxial surface or glabrous and long-pilose toward the base, the lower margins ciliate, otherwise glabrous. *Inflorescences* terminal, exserted, peduncle terete, ca. 20 cm long, hispid, densely pilose toward the distal portion near the junction with the panicle; *panicles* lax, diffuse, multiflowered, 4–12 cm long, 3.5–10 cm wide; *main axis* flexuous, hispid, the pulvini pilose; first-order branches alternate, divergent, the axis of the branches triquetrous, greenish to purplish, scabrous and sparsely hispid, spikelets solitary on second- or third-order branches; pedicels triquetrous, scabrous. *Spikelets* ellipsoid, (2.2–)2.4–2.8 mm long, 1–1.1 mm wide, greenish to purplish, plano-convex, sparsely hispid or glabrous, the upper glume and lower lemma subequal, as long as or shorter than the upper anthecium. *Lower glume* 1.2–1.4 mm long, ⅓–½ the length of the spikelet, obtuse, 1-nerved, not embracing the upper glume. *Upper glume* 7–9-nerved. *Lower lemma* glumiform, 7-nerved. *Lower palea* lanceolate, 1.5 mm long, 0.4 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* narrowly ellipsoid, 2.4–2.5 mm long, 0.9–1.1 mm wide, whitish, smooth, shiny, indurate, papillose, apiculate and short-pilose and with a green spot on the apex of the lemma. *Caryopsis* ellipsoid, 1.6 mm long, 1 mm wide; hilum punctiform, embryo less than ½ the length of the caryopsis.

*Distribution and ecology:* Mexico to El Salvador, and Ecuador, on forest edges, in moist places, between 550 and 2,400 m.

*Additional specimens examined.* ECUADOR. LOJA: Argelia, 2,300 m, *Espinosa 547* (US). EL SALVADOR. SANTA ANA: Hacienda San José, *Rohweder 2111* (MO). GUATEMALA. ALTA VERAPAZ: along route ca. 14 mi. between Cobán and Tactic, 6 mi. S of Cobán, 13 mi. N of Tactic, *Croat 41422* (MO). BAJA VERAPAZ: along highway ca. 14 to Cobán, about 1 mi. S of turnoff to Salama, *Croat 41154* (MO). HUEHUETENANGO: pine-oak forest in canyon of Río Chixoy near Malacatancito about 20 km SW of Huehuetenango, 1,600 m, *Williams et al. 22170* (US), *22171* (F). QUEZALTENANGO: Chiquival, 2,360 m, *de Koninck 117* (US). HONDURAS. 17 km NE of Nueva Ocotepeque, *Harmon & Dwyer 3771* (MO). COMAYAGUA: 75 km E de Comayagua, *Hernández 198* (MO). EL PARAISO: 31 km S of El Zamorano, on road between Guinope and Mandasta, *Pohl & Davidse 12152* (MO); edge of bog in mixed oak-pine forest near Piedra Herrada, 1,500 m, *Williams 15983* (US). FRANCISCO MORAZAN: Universidad, Campo abierto, *Lainez 91* (MO); W slope of Cerro de Uyuca, along trail from Las Flores toward Tatumbla, 1,600 m, *Standley 22813, 23466* (US); SW of San Juancito, *Pohl & Davidse 11984* (MO); Jutiapa, ca. 7 km NE of Tegucigalpa, *Pohl & Davidse 11977* (MO); La Tigra, 35 km NE de Tegucigalpa, *Ordoñez 42* (MO). OCOTEPEQUE: alrededores de Belén Gualcho, *Nelson et al. 4026* (MO). MEXICO. CHIAPAS: Mun. Siltepec, on the ridge above Siltepec on the road to Huixtla, *Breedlove & Almeda 58273* (MO). OAXACA: 56 km de Tlaxiaco rumbo a Putla, *Beetle M-4807* (MO).

This species is related to *P. viscidellum*, differing in its larger spikelets (2.2–)2.4–2.8 mm long. It is also related to *P. divergens*; the latter species lacks a conspicuous pseudoligule and usually has sparsely hispid spikelets.

**37. Panicum viscidellum** Scribner, U.S.D.A. Div. Agrost. Circ. 19: 2. 1900. *Dichanthelium viscidellum* (Scribner) Gould, Brittonia 32(3): 357. 1980. TYPE: Mexico. Veracruz: near Jalapa, 1,250 m, 1899, *Pringle 8089* (lectotype, US 354526; isolectotypes, M, MO, P). Figures 18, 19, 20, 30.

*Panicum tremulosum* Mez, Notizbl. Bot. Gart. Berlin-Dahlem 7: 76. 1917. TYPE: Venezuela. Distrito Federal: prope Caracas, *Moritz s.n.* (holotype, B; fragment, US).

*Panicum longiculme* Swallen, J. Wash. Acad. Sci. 21: 15. 1931. TYPE: Colombia. Antioquia: Quebrada del Alto, in mountains above Bello, 17 June 1930, *Archer 160* (holotype, US 1445529).

*Panicum blakei* Swallen, Contr. U.S. Natl. Herb. 29: 422. 1950. TYPE: Guatemala. Izabal: along trail from Los Amates to Izabal, Cerro de Las Minas, 31 May 1919, *Blake 7817* (holotype, US 1163068).

*Panicum furtivum* Swallen, Contr. U.S. Natl. Herb. 29: 421. 1950. TYPE: Guatemala. Huehuetenango: between Quetzal and Barillas, Sierra de los Cuchumatanes, 1,600–2,000 m, 18 July 1942, *Steyermark 49123* (holotype, US 1935043).

Short-rhizomatous perennial. *Culms* decumbent, rooting and branching at the lower nodes, then erect, branching at the upper nodes, 15–100 cm tall; internodes 3.5–18 cm long, hollow, striate, compressed, hispid, with long, rigid hairs; nodes compressed, densely pilose with whitish, retrorse hairs. *Sheaths* 2.5–13.5 cm long, papillose-pilose with tuberculate, caducous hairs, the margins ciliate. *Ligules* short-membranous at the base, then long-ciliate, 0.3–1(–2) mm long, with a conspicuous pseudoligule with hairs 2–3 mm long; collar pilose. *Blades* ovate-lanceolate to lanceolate, 3–14 cm long, 0.4–2 cm wide, glabrous or short-pilose on both surfaces, the base cordate and clasping, the apex acute, the margins long-ciliate and scabrous. *Inflorescences* terminal, exserted or partially included within the upper leaves, peduncle flexuous, 10–23 cm long, glabrous or sparsely or densely hispid; *panicles* diffuse, 3–12 cm long, 2–

10 cm wide; *main axis* glabrous or densely hirsute; pulvini pilose and scaberulous, first-order branches alternate to subopposite, ascendent and divergent, the axis of the branches glabrous or hispid, eglandular. *Spikelets* solitary, ellipsoid, (1.5–)1.8–2(–2.2) mm long, 0.7 mm wide, sparsely pilose, occasionally glabrous, the upper glume and lower lemma subequal, the stipe absent. *Lower glume* ovate, 0.6–1 mm long, ⅓–½ the length of the spikelet, sparsely pilose, acute, nerveless to 1–3-nerved, not embracing the upper glume. *Upper glume* 1.4–1.8 mm long, 7–9-nerved. *Lower lemma* glumiform, 7-nerved. *Lower palea* 0.7 mm long, 0.2 mm wide, hyaline, glabrous; lower flower absent. *Upper anthecium* ellipsoid, 1.5–1.8 mm long, 0.6 mm wide, indurate, papillose, shortly apiculate, apicule puberulous; stamens 3, the anthers 0.8 mm long. *Caryopsis* ellipsoid, 1.2 mm long, 0.6 mm wide, hilum punctiform, embryo ½ the length of the caryopsis.

*Distribution and ecology:* from Mexico and the West Indies to northern South America, in Colombia, Ecuador, and Venezuela. Commonly found on forest edges, roadsides, and riverbanks, in moist places among shrubs, between 100 and 2,800 m.

*Selected specimens cited.* BELIZE. BELIZE: Ridge Lagoon Plantation ca. 12 mi. NW of Belize, *Croat 24077A* (MO). EL CAYO: Mountain Pine Ridge, along Coona Cairn Road, *Davidse & Brant 33022* (MO). STANN CREEK: Pine Ridge, *Gentle 8491* (US). TOLEDO: lower part of Richardson Creek, affluent of Bladen Branch, 100–250 m, *Davidse & Brant 32336** (MO, SI). COLOMBIA. ANTIOQUIA: Mun. Salgar, km 15 of road Salgar–El Dauro, 5°59′N, 76°07′W, *Zarucchi et al. 5957* (MO). BOYACA: Reserva Acueducto Villa de Leyva, 2,100 m, *Wood 4426* (COL, K); entre Chinavita y Tibaná, 1,700 m, *Zuloaga 4117* (MO, SI, VEN). CAUCA: La Esmeralda, near Jamundí, *Pittier 940* (US); El Tambo, *von Sneidern 1305* (G); without locality, *Zuloaga & Londoño 4203** (SI). CUNDINAMARCA: subida al Alto del Tigre, 1,700 m, *Zuloaga 4027* (COL, MO, SI); Quetame, *Zuloaga 3962* (COL, MO, SI). EL VALLE: Monte Frío, Yanaconas, 1,700–1,850 m, *Killip & García 33718* (COL, US). MAGDALENA: Sierra Nevada de Santa Marta, región del Campano, 1,300 m, *Barkley & Gutiérrez 1918* (COL, US). NARIÑO: Mun. Junín, 1,100 m, *Pinto et al. 1889* (COL); La Florida, *Archer 3314* (COL); Reserva La Planada, Quebrada El Mar–La Calladita, *Olga de Benavides 9533* (MO). NORTE DE SANTANDER: road from Pamplona to Toledo, crossing the divide between Río La Teja and Río Mesme, 2,500–2,800 m, *Killip & Smith 19812* (MO, US). SANTANDER: Mesa de los Santos, 1,500 m, *Killip & Smith 15106* (US). TOLIMA: "La Trinidad," Líbano, *Pennell 3323* (US). VALLE DEL CAUCA: La Cumbre, 1,600 m, *Pennell & Killip 5671* (NY), *Pennell 5020* (NY). COSTA RICA. ALAJUELA: 15 km NNW of San Ramón by road, 2.5 km N of Balsa on road to San Lorenzo, *Liesner & Judziewicz 14878* (MO, SI). CARTAGO: ca. 8 km S of Cartago by air, Finca El Chaparral, 4.5 km S of bridge on Agua Caliente at Lourdes, *Liesner & Judziewicz 14619* (MO); 3 km S of Agua Caliente, 1,400 m, *Pohl & Davidse 11376* (US). GUANACASTE: Parque Nacional Rincón de la Vieja, SSE slopes of Volcán Santa María above Hacienda Santa María, 900–1,200 m, *Davidse et al. 23439* (MO, SI). PUNTARENAS: Las Alturas along Río Coton, *Davidse 24132* (MO, SI). SAN JOSE: Cordillera de Talamanca, 14 km S of División along the Interamerican highway, 1,500 m, *Pohl & Davidse 11618* (US). CUBA. ISLA DE LA JUVENTUD: Columbia, *Ekman 12406* (US). ECUADOR. TUNGURAHUA: valley of Pastaza River, between Caños and Cashurco, 8 hr. E of Baños, 1,300–1,800 m, *Hitchcock 21809* (US); valley of Río Pastaza, Hacienda Río Verde Grande, *Asplund 7839* (G, K, US); Agoyán, *Asplund 7627* (MO). EL SALVADOR. CHALATENANGO: pass on Hwy. 4, 7 km SSE of La Palma, *Pohl & Davidse 11889* (MO). GUATEMALA. ALTA VERAPAZ: Cobán, 1,350 m, *von Tuerckheim 3836* (M); savanna on S side of Cerro Chinaja, between Sachaj and Sacacac, 150–180 m, *Steyermark 45168* (US). BAJA VERAPAZ: Biotopo del Quetzal, WNW of Purulha, *Stevens et al. 25420** (MO); 4 km N of El Chol, *Harmon & Dwyer 3127* (MO). HONDURAS. ATLANTIDA: valley of Río Cangrejal, 17 km SSE of La Ceiba, *Pohl & Davidse 12084* (MO). COMAYAGUA: 14 km SE of Taulabe by road, *Pohl & Davidse 12112* (MO). EL PARAISO: Cerro Monserrat, cerca de Yuscarán, *Nelson & Romero 4267, 4279* (MO); 32 km W of Danli along Hwy. 4, *Pohl & Davidse 11928* (MO). GRACIAS A DIOS: Caserío de Rus-Rus, vaguada del Río Rus-Rus, *Nelson & Romero 4097* (MO). LA PAZ: Agua Blanca River, between Chinacla and Planes de Mulle, *Molina & Molina 24346* (MO). FRANCISCO MORAZAN: Río del Gallo, near El Jicarito, 2 km from El Zamorano, *Swallen 10992* (MO); 2.5 km N of Zambrano on road to San Francisco de Soroguara, *Pohl & Davidse 12136* (MO); 14 km S of El Zamorano on road to Guinope, *Pohl & Davidse 12147* (MO). OLANCHO: Montaña Los Zapotes, 10 km noroeste campamento, *Martínez 37* (MO). SANTA BARBARA: Trinidad, Finca Las Colmenas, *Salguero 15* (MO). JAMAICA. Banana Ground, *Adams 10098* (MO). MEXICO. CHIAPAS: Lago Pojoj, Lagos de Montebello National Park, *Breedlove & Davidse 55022* (MO); Mun. La Trinitaria, Lago Tziscao, Lagos de Montebello National Park, *Breedlove & Davidse 55031* (MO). OAXACA: Mun. San Pedro Yaneri, Distr. Ixtlán, 17.3 km S of La Esperanza and 40.3 km SE of Valle Nacional, 1,900 m, *Davidse et al. 30257* (MO). VERACRUZ: about 7 mi. SSE of Jalapa in area of rolling hills, *Reeder & Reeder 6000* (MO); Orizaba, *Hitchcock s.n.*, Amer. Gr. Hb. 179 (MO). NICARAGUA. ESTELI: Cerro Tisey, faldas del lado S, 1,300–1,400 m, *Moreno 9670* (MO, SI). GRANADA: Volcán Mombacho, lado N, arriba de Finca El Progreso, *Neill 868* (MO). JINOTEGA: along Hwy. 3 ca. 1.9 km NW of Aranjuez road entrance, *Stevens 5576, 5591* (MO). MATAGALPA: Santa María de Ostuma, Cordillera Central de Nicaragua, between Matagalpa and Jinotega, 1,300–1,500 m, *Williams et al. 23591* (F, US). NUEVA SEGOVIA: El Cincho, a 8 km al NE de El Jícaro, *Moreno 19510* (MO). RIVAS: Isla Ometepe, Volcán Concepción, costado NW del volcán, punto de referencia a "Los Hatillos," *Robleto 214* (MO). ZELAYA: near Tala Has and Puente Mango (over Río Kisalaya), *Stevens 7650* (MO). PANAMA. CHIRIQUI: Foothills, vicinity of El Boquete, *Hitchcock 8178* (SI). PANAMA: top of Cerro Jefe, 2.3 km N of Panamerican highway, *Folsom et al. 2534* (MO). VENEZUELA. ANZOATEGUI: Distr. Freites, Cerro Peonia, above Los Pajaritos, 31 airline km NE of Bergantín and

N of Mundo Nuevo, Serranía de Turimiquire, 1,400–1,700 m, *Davidse & González 19914* (MO, VEN). ARAGUA: Distr. Ricaurte, cerca de Colonia Tovar, a 0.6 km del desvío al Jarillo vía Colonia Tovar, *Zuloaga & Ortíz 4279*, 4281* (MO, SI, VEN); Parque Nacional Henry Pittier, *Zuloaga & Ortíz 4530*, 4532*, 4537** (MO, SI, VEN); Distr. Ricaurte, 0.5 km del desvío a Buenos Aires, *Zuloaga et al. 4288* (MO, SI, VEN). COJEDES: Cerro Azul, Fila La Blanquera, al NE de La Sierra, 1,100 1,300 m, *Delascio 7535* (VEN). DISTRITO FEDERAL: Cordillera Costanera, El Junquito, *Chase 12427* (K, VEN), *12428* (US), *12431, 12440* (US, VEN), *12441* (US); Piso de El Avila, *Alston 5561a* (MO); Parque Nacional El Avila, ridgetop in vicinity of Lagunazo, between Pico El Avila and Pico Occidental, 2,200 m, *Nee & Whalen 16805* (F, VEN). FALCON: Sierra de San Luis, entre Curimagua y San Luis, 1,300–1,400 m, *Steyermark 99143* (M, US, VEN). LARA: Distr. Iribarren, El Cortijo, *Burandt Jr. V0570* (MO, US). MERIDA: Capellanía (Bailadores), 1,600 m, *Tamayo 2362* (VEN). MIRANDA: 34 km NW of Santa Lucía by road, *Davidse 2912* (MO). TACHIRA: between Las Delicias and Paraguita, bordering Río Táchira, *Steyermark 57148* (US).

*Panicum viscidellum* is a common species with some degree of variation in the size of leaves and pilosity, characters that were used for describing *P. tremulosum*, *P. blakei*, and *P. furtivum*. *Panicum viscidellum* is related to *P. sciurotoides* and *P. umbonulatum*, differing from the first species by the presence of a conspicuous pseudoligule and its usually larger spikelets, and from *P. umbonulatum* by its smaller spikelets.

Pohl (1980) noted that the correct name for this species might be *Panicum reflexopilum* Steudel, Syn. Pl. Glumac. 1: 84. 1853 (described from Oaxaca, Mexico). However, neither he nor we could find the type specimen of *P. reflexopilum*, so the name remains dubious.

All specimens examined for anatomical purposes have a leaf anatomy typical of section *Dichanthelium*, including numerous macrohairs, either cushion-based (Fig. 18D) or with few modified epidermal cells associated with the hair bases (Fig. 19A–D). Several of the specimens exhibit an unusual silicification of the basal cells associated with the macrohairs (Fig. 20). The hairs themselves may be lost but the modified, swollen basal cells are then clearly seen to contain opaline silica deposits (Fig. 20F).

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Nash 1243 (1a); 1337 (23); 2076 (23). Nee 10694 (37); 16805 (37); 23182 (29a); 26237 (18); 26325 (2a). Neill 868 (37). Nelson 634 (2a); 656 (2a); 1005 (32); 3618 (36); 3800 (13); 3842 (32); 4026 (36); 4097 (37); 4267 (37); 4279 (37); 4708 (32). Nicora 3067 (25a); 4170 (25a); 5903 (25b); 6027 (25b); 6530 (25b). Noblick 2472 (27); 2735 (26); 2870 (10).

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Quarín 1593 (25b); 1653 (25b); 1744 (25b); 2872 (25b); 3171 (25b); 3200 (25b); 3205 (25b).

Rambo 29194 (25b); 29573 (25a); 34202 (25b); 38181 (25a); 44279 (25a); 44638 (25b); 44677 (25b); 53841 (33); 54088 (25b); 54532 (25a). Ramia 140 (37). Ramírez Reyes 2513 (1a). Reeder 6000 (37); 6079A (29a). Regnell III-1358 (20). Reiche s.n. (25b). Reitz 1978 (25a); 2595 (25b); 3225 (25c); 3626 (27); 5157 (25b); 5159 (25b); 5278 (25b); 5279 (33); 5449 (33); 5561 (15); 7962 (33); 10291 (33); 10362 (33); 11358 (34); 12796 (34). Renvoize 2929 (25a); 3034 (25b); 3109 (25b); 3150 (25b); 3743 (25b); 4072 (25a); 4307 (27). Riedel s.n. (25a); s.n. (25b); s.n. (26); 226 (30); 228 (27); 2151 (20); s.n. (15). Robleto 214 (37). Roca 7944 (1a). Roe 2079 (13). Rohweder 2053 (36); 2111 (36); 2264 (36). Roig 2205 (13). Roldán 289 (2a). Rombouts s.n. (27). Romero-Castañeda 1443 (2a). Rondón s.n. (11); s.n. (24). Rose 21134 (27). Rosengurtt s.n. (25b); B-241 (25b); B-247 (25b); B-739 (25b); B-2722 (25b); B-5077 (25b); B-6217 (25a); 6930 (25b); 9001 (25b); 9253 (25b); 11329 (25a). Rotman 61 (25b). Rubio 71 (29a); 77 (29a); 78 (29a). Rzedowski 1158 (13).

Salguero 15 (37). Salzmann 697 (27). Sampaio 1608 (25b); 4699 (27). Sandwith 1359 (24). Santos 2687 (25b). Saravia 4363 (1a). Sánchez Vega 2295 (24). Scala s.n. (25a). Schaffner 146 (2c). Schenck 229 (27). Schinini 2423 (25b); 2583 (25b); 8775 (25b); 11374 (25b). Schnem 1605 (25b). Schwacke 13153 (27); 14409 (25b). Schwarz 4979 (25b); 6756 (25b). Scolnik s.n. (2a). Segadas-Vianna 650 (30). Sellow 523 (34). Sendulsky 321 (15); 424 (33); 446 (16); 593 (25b); 686 (25b); 693 (15); 711 (25b); 712 (25b); 723 (15); 739 (25a); 768 (25a); 842 (25a); 947 (15); 1058 (25b); 1063 (33); 1166 (25b); 1200 (15); 1373 (15); 1609 (16); 1920 (16). Seymour 4576 (2b); 4605 (32); 4741 (2b); 4742 (32); 4743 (2b); 5853 (2a); 5978 (2b); 5979 (2b); 7639 (37). Shafer 3001 (12a); 3018 (28); 3083 (32); 3481 (28); 3531 (1a); 10484 (1b); 10639 (1a); 10873 (1a); 11021 (29b); 11049 (1b). Sharp 45928 (18). Shnee 484 (15). Sintenis 355 (2a); 1224 (1a); 5985 (1a). Skutch 524 (13). Skvortzov 19 (25b). Smith 163 (32); 441 (25b); 2140 (2a); 6107 (25b); 7314 (33); 7334 (30); 7640 (33); 7825 (33); 8059 (25b); 8664 (25b); 8710 (34); 10899 (33); 12534 (25b); 12712 (25b); 12792 (25b); 13066 (25b); 13484 (25b); 14008 (33); 14305 (25b); 15456 (33); 15464 (25a); 15478 (25b); 15491 (25b); 15523 (33); 15549 (33); 15558 (25b); 15629 (25b); 15680 (25b); 15737 (25b); 15809 (33); 15889 (33); 15896 (25b). Soderstrom 960 (37); 960a (1a); 968 (37). Solomon 1300 (27); 4091 (25b); 9523 (27). Soto 44 (18). Souza Santos 88 (27). Spegazzini s.n. (25b). Standley 22811 (29a); 22813 (36); 23466 (36); 28256 (2a); 28745 (1b); 29366 (1a); 34048 (2a); 39320 (2a); 43377 (2a); 56009 (1a); 56261 (2a); 64360 (2c); 65681 (2c); 69059 (12a); 71468 (2a); 82760 (2c); 89929 (2a). Stern 1180 (2a). Stevens 4118 (2a); 5576 (37); 5578 (18); 5591 (37); 7649 (32); 7650 (37); 7816 (32); 12809 (32); 14796 (2c); 14802 (29a); 17972 (2c); 18103 (18); 18000 (29a); 18105 (37); 25420* (37); 25467 (18). Stevenson 2783 (23). Steyermark 29707 (1a); 42418 (1a); 42770 (12a); 43463 (19); 43942 (12a); 44005 (18); 45168 (37); 47958 (2a); 49025 (2a); 56978 (1a); 57148 (37); 59906 (24); 75642 (24); 85862 (1a); 85871 (1a); 87974 (24); 88596 (27); 89073 (15); 93883 (24); 94668 (12a); 97638 (27); 99143 (37); 99396 (37); 99468 (37); 104200 (24); 105858 (1a); 106199 (27); 109377 (24); 117547 (27); 121762 (15); 127736 (37); 127739 (37); 128196 (24). Strang 833 (33). St. Hilaire 296 (34); 323 (27). Sucre 1738 (15); 1955 (15); 2089 (15); 2317 (33); 3116 (25b); 4017 (25b); 5349 (4); 9087 (25b). Sullivan 185 (37). Svenson 4486 (2b). Swallen 4303 (26); 4531 (24); 4539 (26); 4677 (26); 4823 (26); 7034 (25b); 7211 (25b); 7406 (25b); 8064 (25b); 8125 (25b); 8140 (25a); 8419 (25b); 8571 (25b); 9076 (25a); 9252 (25a); 10824 (37); 10895 (36); 10952 (37); 10992 (37); 11012 (2a); 11018 (36); 11021 (36); 11034 (36); 11047 (36); 11048a (36); 11070 (37); 11075 (2a); 11287 (2c); 11299 (2a); 11324 (37); 11356 (2a); 11357 (37); 11376 (37); 11397 (37); 11411 (37). Sytsma 1462 (37); 3221 (32).

Tamayo 114 (1a); 1625 (37); 1861 (2a); 2362 (37); 49885 (37). Tate 281 (4). Tavares 788 (26). Taylor 127 (18); 11842 (18); 11868 (37). Tenorio 66-197 (26). Tharp 43164 (19). Thomas 2794 (18). Tillett 27 (2a). Toro 290 (2a); 353 (2a). Torres 2020 (18). Tracy 9074 (1b); 9078 (2a). Trejos 190 (1a). Troncoso 2020 (25a); 2670 (25a); 2707 (25a); 2709 (25a); 2802 (25a); 3253 (25a). Trujillo 346 (37); 826 (37). Tucker 1056 (29a). Tyson 4436 (37).

Ule s.n. (33); 664 (33). Underwood 955 (23).

Valeur 4 (23); 293 (18). Valls s.n. (25b); 1114 (25b); 1178 (25b); 1398 (25b); 1651 (25b); 1664 (25b); 1665 (25b); 1780 (25b); 1809 (25b); 1870 (33); 2308 (25a); 2361 (25b); 2903 (33); 10087 (25c). van der Werff 6167 (32). Vasconcellas s.n. (27). Vázquez Avila 189 (25b). Venturi 8428 (25b); 9545 (25b); 9691 (25b). Vianna 650 (30). Victorin 21448 (29b). Vidal II-6467 (9); II-6485 (9). Villela 48 (29a). von Sneidern 1305 (37). von Tuerckheim II-1322 (12a); 3059 (18); 3321 (23); 3836 (37).

Warming s.n. (20). Wawra 970 (15). Weberling 719 (37). Webster 25725 (10). Whitefoord 2407 (2b). Wilbur 14916 (18). Wiley 464 (1b). Williams 12076 (36); 14813 (1b); 15602A (2a); 15983 (36); 17130 (36); 18842 (1b); 22170 (36); 22171 (36); 23591 (37); 23906 (1a); 31265 (2a); 41919 (37). Wingfield 5415 (37); 6471 (1a); 6483 (37); 6707 (12a); 6844 (12a); 7124 (12a); 8518 (32). Wood 3660 (37); 3861 (37); 4426 (37); 5352 (1a). Woodbury s.n. (23). Woolston G-117 (25b). Wright 3467 (28); 3874 (2a).

Zarucchi 5957 (37); 5958 (2a). Zehntner 248 (31); 263 (31); 2017 (31); 2048 (31). Zuloaga 444 (25b); 463 (25b); 486 (25b); 554 (25b); 765 (25b); 1081 (25a); 1579 (25b); 1891 (25b); 1972 (25b); 2060 (25b); 2128 (25b); 2349 (27); 2351* (30); 2352* (25b); 2354* (27);

2358* (30); 2361* (25b); 2363 (30); 2373* (15); 2374* (33); 2380 (25b); 2382 (30); 2389 (30); 2390* (15); 2409 (27); 2423 (15); 2425 (15); 2427 (27); 2469* (4); 2490 (2a); 2492 (2a); 3079 (25b); 3085 (25b); 3191 (25b); 3228 (25b); 3231 (25a); 3409 (25b); 3846 (25b); 3852 (25a); 3857 (25a); 3859 (25b); 3860 (25b); 3861 (25b); 3864 (25a); 3962 (37); 4025 (2a); 4035* (29a); 4027 (37); 4117 (37); 4119 (2a); 4120 (2a); 4184* (37); 4201* (1a); 4202* (2a); 4203* (37); 4279* (37); 4280* (29a); 4281 (37); 4288 (37); 4399 (27); 4404* (24); 4406* (11); 4408 (4); 4427* (11); 4470* (4); 4474 (24); 4475* (27); 4530* (37); 4532* (37); 4534* (15); 4537* (37); 4543 (25b); 4544 (25b).

# A REVISION OF *MONNINA* SUBG. *PTEROCARYA* (POLYGALACEAE) IN NORTHWESTERN SOUTH AMERICA[1]

*Bente Eriksen*[2]

ABSTRACT

Three subgenera are currently recognized in the genus *Monnina*, which consists of approximately 175 species. This paper treats the systematics of *Monnina* subg. *Pterocarya* in northwestern South America. The subgenus is a naturally coherent taxon characterized by dry, samaroid fruits. It consists of ca. 25 species, 11 of which occur in the area concerned.

The genus *Monnina* was established by Ruíz & Pavón (1798) and was dedicated to José Moñino, the count of Floridablanca. It comprises fruticose species with drupaceous fruits, as well as herbaceous ones with more or less winged samaras. De Candolle (1824) described the section *Pterocarya* to accommodate the species that have the fruit margin expanded into a membranaceous wing. This division, however, is artificial because it neglects a number of species with samaras, where the wing is small or completely lacking. Chodat (1896) realized this and emended section *Pterocarya* DC. to comprise all annual or perennial herbs with samaras and gave the taxon subgeneric rank. The genus *Monnina* comprises ca. 175 species, ca. 25 of which belong to the subgenus *Pterocarya*.

Species of *Monnina* subg. *Pterocarya* have never been revised as a group. The works of Chodat (1894, 1896, 1909, 1915, 1934), Chodat & Wilczek (1902), and Ferreyra (1990) mostly included various descriptions of new species, and those of Ferreyra (1946, 1953) and Grondona (1945) were entirely floristic. The aim of the present paper is to give an extensive treatment of the subgenus in the northern Andes. Here, the southern limit of the northern Andes is defined as the Peruvian border with Chile and Bolivia. This geographical boundary coincides with a natural phytogeographical boundary (Molau, 1988). A revision of the remainder of the species is in preparation.

## ECOLOGY AND GEOGRAPHICAL DISTRIBUTION

Plants of *Monnina* subg. *Pterocarya* are confined to semiarid habitats. The distribution is disjunct, with a western and eastern territory in South America and an exclave in Mexico and the southwestern United States. The western territory is found along the coast of the Pacific Ocean and in the mountains from southern Ecuador to central Chile, extending into western Bolivia and Argentina. The eastern territory covers northeastern Argentina, southern Paraguay, Uruguay, and the dry parts of southeastern Brazil, principally east of Río Paraná (Fig. 1). The map shows the narrow gap in the South American distribution area directed north-south through Argentina. The gap coincides with the extensive plain occupied by the Larrea Desert of Gran Chaco and adjacent areas (Walter, 1979) and is probably too dry to be favorable for *Monnina*. Grondona (1945) noticed the absence of *Monnina* in this particular area and established, as a consequence, their preference for mountainous habitats. He did not exclude the possibility that specimens might be collected there in the future. Since Grondona wrote the Flora, however, no spec-

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FIGURE 1. Distribution of *Monnina* subg. *Pterocarya*.

imen has been found in that area. The fact that different species occur on either side of the gap supports the assumption that the plain serves as a barrier. To the north, the two territories are delimited by areas with higher humidity or, in the Planalto do Mato Grosso, by periodical flooding. The coastal desert of Peru is, like the Gran Chaco, very dry and should be unsuitable for *Monnina* species, but here the "garua," or fog blanket, caused by the cold sea current off the Peruvian coast, plays an important role. Even though the precipitation is not measurable, a considerable amount of water is yielded through fog (Walter, 1979).

Only one species occurs north of the equator, viz *M. wrightii* in Mexico and the southwestern United States, but the same species is abundant in Bolivia and Argentina and has probably been introduced to Mexico.

The semiarid habitats to which the species are confined are usually devoid of dense and tall vegetation. In some areas of southern Ecuador the natural vegetation is mainly dense shrubland, and competition for light does seem to be a limiting factor. The *Monnina* species here are always confined to open grassland, natural or artificial.

Flowering begins near the end of the rainy season and continues 3–9 months. In habitats with sporadic rainfall, the flowering season is variable and flowering occurs whenever humidity allows it.

The altitudinal range of *Monnina* is rather wide, sometimes even within species. In most cases, however, two species sharing latitude are usually separated altitudinally with little or no overlap.

As the different species are rarely sympatric, it is not surprising that no specimens have been found that could be interpreted as hybrids. Besides, the pollination mechanism in *Monnina* is likely to prevent interspecific pollination. The flowers are pollinated by bumblebees. On landing, the insect presses the released pollen through an opening near the

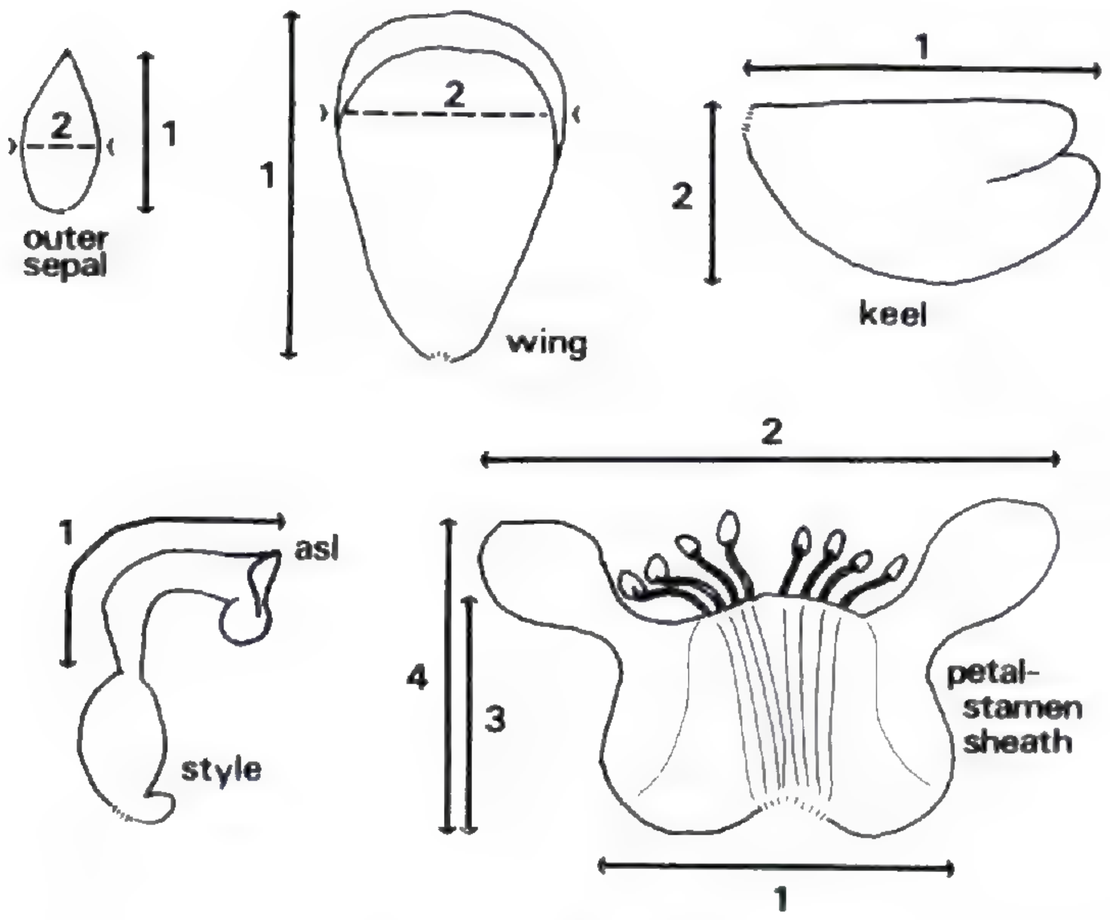


FIGURE 2. Floral structures showing the way in which the various parts were measured. Outer sepal, wing, and keel given as *1* × *2*. Style length *1*. Petal-stamen sheath given as *1/2* wide, *3/4* high. asl = anterior stylar lobe.

apex of the keel and at the same time foreign pollen is deposited on the stigma. Because the species differ greatly in flower size and stigma position, only a flower of the same species gets pollinated, even if the insect visits another species during a foraging bout.

## MATERIALS AND METHODS

This study is based on herbarium specimens, pickled material, and fieldwork. Field studies were carried out in 1987–1988 in Ecuador and northern Peru. Five species of *Monnina* subg. *Pterocarya* were seen in the field.

### MEASUREMENTS

Measurements were taken on the leaves of the main axis (leaves on the branches are generally smaller). The measurements are given in the descriptions as length × width. For the inflorescence, the main one was measured (inflorescences on the branches are shorter). Inflorescences that have started to fruit were selected, since the inflorescence axis elongates during flowering.

The pedicel was measured when carrying an open flower.

The flower parts measured were taken from the bud just above the youngest unfolded flower. This choice ensures intact flower parts and still gives a relatively good picture of the flower size. The way in which the various flower parts were measured is shown in Figure 2. In the descriptions, measurements for the petal-stamen sheath are given as "width at base"/"width across petal lobes" and "length of filament sheath"/"total length including petal lobes."

Fruit size is given for mature fruits.

Vegetative parts of dry material were measured. My experiments have shown that leaves of *Monnina* shrink approximately 10% in the drying process. The descriptions have not been corrected for shrinkage. Flowers are measured on rehydrated material, except for a few specimens of which I have pickled material.

### TERMS

The nodal glands present in some species of *Monnina* are traditionally, and so also here, called stipules, although they are not homologous with stipules.

The construction of the flower in *Monnina* is quite extraordinary, and this type of papilionaceous flower is unique for the Polygalaceae. Figure 2 shows the floral parts and the terms used for each.

## SYSTEMATICS

**Monnina** subg. **Pterocarya** (DC.) Chodat, Bull. Herb. Boissier 4: 251. 1896. *Monnina* sect. *Pterocarya* DC., Prodr. 1: 340. 1824. TYPE: *Monnina pterocarpa* Ruíz & Pavón, lecto-type here designated.

Annual or perennial herbs. Leaves alternate, short-petiolate to subsessile, with or without stipules. Stems and branches terete, covered by unicellular hairs, either white, conical and curved or compressed and straight, or yellowish with knoblike thickenings on their outer side and ± straight. Laminae simple, pinnately veined, entire or rarely undulate. Flowers arranged in simple racemes, each subtended by a bract and two bracteoles, irregular; outer sepals 3, small, herbaceous, free or rarely the lower two shortly connate at base; inner sepals (wings) 2, large, lateral, petaloid; petals 3, the lower (keel) carinate, the upper two united in their lower part with the filament sheath (see below), but free from each other, forming a conduplicate petal-stamen sheath; stamens diadelphous, (4–)6–8, the filaments fused for most or all of their length into a filament sheath to which lateral margins the upper petals are adnate; style compressed, geniculate to gently curved, apically unequally cleft, the posterior lobe with a sessile or ± stalked capitate or discoid stigma, the anterior lobe sterile, often forming a tooth. Ovary 1- or 2-locular, subtended by a glandular disc enlarged toward the adaxial side into a knoblike process. Fruit a regularly or irregularly winged, or occasionally wingless samara.

KEY TO THE SPECIES OF *MONNINA* SUBG. *PTEROCARYA* IN NORTHWESTERN SOUTH AMERICA

1a. Stipules absent.
2a. Stamens 8, the filaments free in the upper part, or anthers seemingly sessile.
3a. Fruit villous.
4a. Perennial, the leaves linear, ericoid ..... 1. *M. fosbergii*
4b. Annual, most leaves rhomboid, not ericoid.
5a. Stem and branches erect, wings and keel bright blue, the keel yellow apically, anterior stylar lobe a blunt tooth ..... 2. *M. leptostachya*
5b. Stem and branches ascending, wings pale blue, the keel pale yellow throughout, anterior stylar lobe a pointed tooth ..... 3. *M. polygonoides*
3b. Fruit glabrous or pubescent.
6a. Filaments free in the upper part ..... 4. *M. ramosa*
6b. Filaments adnate throughout, the anthers seemingly sessile on the petal-stamen sheath.
7a. Leaves linear, style straight or bent 30°, posterior stylar lobe with a spherical stigma apically ..... 5. *M. macbridei*
7b. Leaves narrowly obovate to narrowly rhomboid, the upper leaves sometimes linear, style bent 80–90°, posterior stylar lobe carrying a bilobed, discoid stigma at base ..... 6. *M. macrostachya*
2b. Stamens 6, sometimes 4 in flowers on branches; in each fascicle some or all filaments fused throughout.
8a. The filaments of the two outer stamens of each fascicle connate throughout, the third free in the upper part or reduced (Fig. 8B), the fruits crescent-shaped ..... 9. *M. wrightii*
8b. The filaments of the three (two) stamens of each fascicle all connate throughout (Fig. 8F), the fruits rotund.
9a. Upper leaves narrowly lanceolate to linear, 0.8–3.7 cm long, obtuse, the inflorescence few-flowered, "torpedo"-shaped in outline ..... 7. *M. amarella*
9b. Upper leaves linear, 2.5–7.0 cm long, acute, the inflorescence many-flowered, very narrowly triangular in outline ..... 8. *M. filifolia*
1b. Stipules present.
10a. Tall plant, usually > 0.5 m, the older parts of stem and branches glaucous, the flowers robust, the stigma a sessile or short-stalked, bilobed disc, the fruit always with a broad, entire wing ..... 10. *M. pterocarpa*
10b. Small plant, usually < 0.5 m, the older parts of stem and branches green or straw yellow, flowers delicate, the stigma resembling a hammer-head (Figs. 9K, 10J), the fruit usually irregularly winged, occasionally wingless or with a narrow, entire wing ..... 11. *M. herbacea*

*Distribution.* Dry lowland and mountainous areas from central Ecuador to central Chile, and from central Brazil to Uruguay; Mexico and the southwestern United States (Fig. 1).

**1. Monnina fosbergii** Ferreyra, Phytologia 69: 356. 1990. TYPE: Ecuador. Loja: S of Oña, above Tablón de Oña, 2,740 m, 21 Feb. 1945, *Fosberg 23204* (holotype, US; isotypes, NY, P). Figure 3.

Perennial herb, decumbent, to 70 cm across, 18–28(–50 fide Barclay & Juajibioy) cm tall, the ascendent branches to 40 cm long crowning the short, woody stem. Branches rooting at nodes, terete, 1 mm diam., furrowed by decurrent leaves, white-pubescent, the hairs curved. Leaves exstipulate; petiole very short or absent; blade narrowly lanceolate to linear, ericoid, coriaceous, 4–13 × 1–1.5 mm, acute at apex, cuneate at base, white-pubescent throughout. Inflorescence few-flowered, narrowly triangular in outline, 11–24 cm long; pedicel 0.5 mm, hirsute; bracts lanceolate, acute, 2.0–3.0 × 0.7–0.8 mm, abaxially hirsute, blue with a green, ciliate margin. Flowers all chasmogamous; outer sepals slightly unequal, the upper one ovate, 1.8–2.0 × 0.8–1.0 mm, arched, the lower narrowly ovate, 1.2–2.0 × 0.7–0.8 mm, all ciliate and blue; wings obovate, 3 × 2 mm, truncate at base, the upper margin ciliate, blue; keel 3 × 2 mm, truncate at base, glabrous, blue with a yellow, emarginate and 2-lobed apex; petal-stamen sheath 2–3/4 mm wide, 1.5–2/2–3 mm high, the petals hirsute adaxially and abaxially on the lower half, the lobes blue, otherwise greenish as the filament sheath; stamens 8, the upper part of the filaments free, glabrous, 1.2–1.5 mm long including the anther, the anther to filament ratio 0.3–0.5; style 1.5–2 mm long, glabrous, bent 45° approximately ⅓ from base; anterior stylar lobe a blunt tooth not exceeding 0.1–0.2 mm in length, the posterior lobe with a sessile or very short-stalked, spherical stigma (Fig. 10A). Fruit 2-locular, narrowly obpyriform with a basal tooth dorsally, 2 × 4 mm when mature, villous, wingless, probably green.

*Distribution.* Probably endemic to the Oña area in Ecuador, ca. 2,800 m (Fig. 6B).

*Specimens examined.* ECUADOR. AZUAY/LOJA: between Oña and Rancho Ovejero, 2,800 m, 1–2 Aug. 1959, *Barclay & Juajibioy 8437* (MO). LOJA: road Oña–

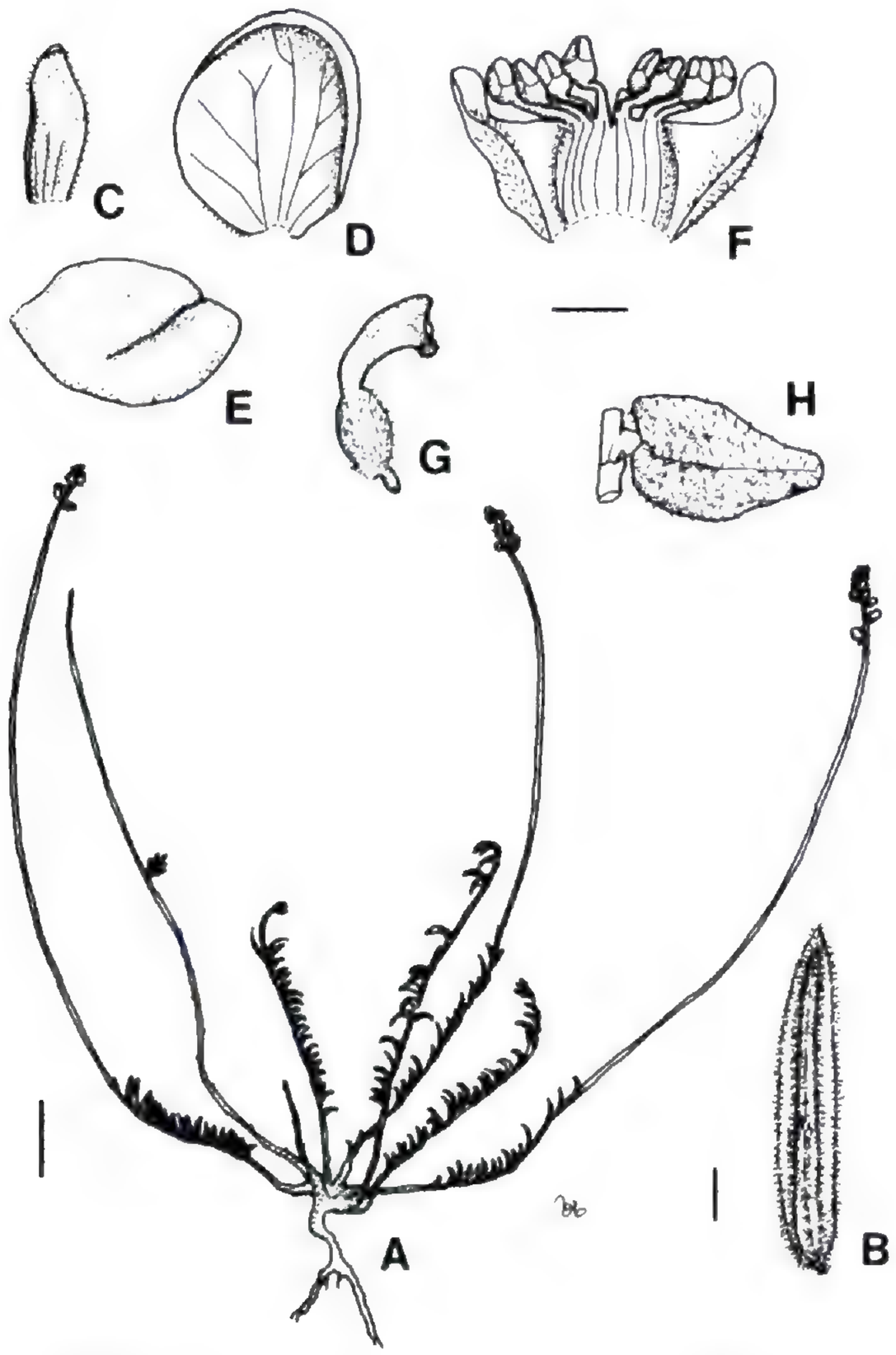


FIGURE 3. *Monnina fosbergii.* —A. Flowering individual. —B. Leaf. —C. Outer sepal. —D. Wing. —E. Keel. —F. Petal-stamen sheath. —G. Gynoecium. —H. Fruit. A–G, *Fosberg 23204* (isotype, NY). H, *Barclay & Juajibioy 8437* (MO). Scales: A = 2 cm. B = 1 mm. C–H = 1 mm.

Saraguro, ca. km 9, 2,800 m, 13 Feb. 1991, *Øllgaard 98803* (AAU, GB, QCA, QCNE).

*Monnina fosbergii* closely resembles the Chilean species *M. linearifolia*, but the floral parts are different. *Monnina fosbergii* has eight stamens, a sessile stigma, and a 2-locular, villous, wingless samara, whereas *M. linearifolia* has six stamens, the stigma at the tip of a very long stalk, and a 1-locular, glabrous, winged samara. Ferreyra (1990), in the original description, compared *M. fosbergii* with *M. filifolia*, to which species it is only distantly related. *Monnina filifolia* has, as the epithet suggests, very narrow leaves, but they are not of the ericoid type. The two species differ in habit and in all essential characters.

Ferreyra (1990) characterized *M. fosbergii* as an erect herb. It is actually decumbent and woody at the base. Perennial species of subgenus *Pterocarya* are common from southern Peru (*M. ramosa*) and southward and in the eastern distribution area, whereas in the north the only perennial representative is *M. fosbergii.* Ferreyra also stated that the ovary is pubescent, which is true only in the broad sense of the word. More precisely, the ovary, and later the fruit, is villous.

**2. Monnina leptostachya** Benth., Pl. Hartw. 125. 1845. TYPE: Ecuador, Loja: near Loja, *Hartweg 713* (lectotype, selected here, K; isolectotypes, NY, P, W). Figure 4.

Annual herb, 15–50 cm, rarely taller. Stem erect, 0.5–3(–4) mm diam., terete or slightly furrowed, unbranched or branched distally, white-pubescent, the hairs curved. Leaves exstipulate; petiole 1–2(–3) mm long, pubescent; laminae on the main axis changing in shape and size from base to apex of the stem; lowermost blades obovate to narrowly obovate, 0.4–4.0 × 0.2–2.0 cm, acute at apex, middle ones rhomboid to narrowly rhomboid, 1.5–6.5 × 0.5–2.5 cm, acute to acuminate at apex, and uppermost blades lanceolate to narrowly lanceolate, 0.8–5.0 × 0.2–1.0 cm, acuminate at apex; all laminae chartaceous, cuneate at base, glabrous except on veins and margin where they are pubescent (in young leaves pubescent throughout). Inflorescence many-flowered, very narrowly triangular in outline, 8–40 cm long; pedicel 0.5 mm long; bracts lanceolate, acute, 1.0–2.0 × 0.3–0.5 mm, less than twice the length of the bud, green, blue, or both colors, ciliate. Flowers all chasmogamous; outer sepals ovate, equal in size or the upper one slightly larger, 1.0–2.0 mm long, ciliate, blue along the margin, otherwise green; wings obovate, 2.5–4 × 2–3 mm, truncate and ciliate at base, bright blue; keel 2.5–4 × 1.5–2 mm, truncate at base, glabrous, bright blue with a yellow, 3-dentate apex; petal-stamen sheath 2–4/4–6 mm wide, 1.5–3/1.5–3 mm tall, the petals hirsute adaxially and at the base abaxially, the lobes bright blue, otherwise greenish as the filament sheath; stamens 8, the upper part of filaments free, glabrous, 0.75–1.25 mm long including the anther, the anther to filament ratio 0:3–0:5; style 2–3 mm long, glabrous, bent 60–90° just above the middle; anterior stylar lobe a blunt tooth, not exceeding 0.1 mm in length, the posterior lobe with a sessile, elongated stigma (Fig. 10B). Fruit 2-locular, ovoid or obpyriform, 1.5–2.5 × 2–3.5 mm, villous, wingless, green, often with purple spots at base or a purple line dorsally.

*Distribution.* Central Ecuador to the Eastern Cordillera of northern Peru. Scattered to locally frequent as a weed in dry scrub, on roadbanks, and among grass in cultivated areas, 1,200–3,000 m (Fig. 6A). It appears after the rainy season and flowers from January to September.

In Peru, *M. leptostachya* has only been collected in Amazonas in the Eastern Cordillera. A similar distribution is shown by *Calceolaria comosa* Pennell subsp. *comosa* (Molau, 1988). The area between the Peruvian and Ecuadorean localities is poorly collected, and it is uncertain whether the distribution is continuous or whether the Peruvian population constitutes an exclave of a disjunct distribution.

*Specimens examined.* ECUADOR. AZUAY: along the Río Tarqui, 4–18 km S of Cuenca, 2,500–2,700 m, 26 Feb. 1945, *Camp E-1836* (NY); near the village of Girón, 2,100 m, 10 Mar. 1945, *Camp E-2199* (F, GH, MO, NY, US); between El Pan and Guachapala, 2,250–2,950 m, 4 Sep. 1945, *Camp E-5263* (NY); Baños, 2,700 m, 17 Sep. 1983, Larsen & Eriksen 45187 (AAU), 2,600 m, 18 July 1939, *Penland & Summers 1058* (GH, NY); Cuenca–Machala road, between Girón and Santa Isabel, km 17 from Girón, 1,800 m, 7 June 1979, *Løjtnant & Molau 14174* (AAU); 10 km S of Gualaceo on road to Sígsig, 2,350 m, 5 Feb. 1988, *Molau, Eriksen et al. 2943* (GB); between Río Molleturo at Huigra and Cruz Pamba, crossing Río Mihuir, N of Molleturo, 1,650–2,300 m, 11 June 1943, *Steyermark 52924* (NY). BOLIVAR: ca. 10 km E of Guaranda, 2,925 m, 25 May 1971, *MacBryde 362* (MO, US). CAÑAR: near San Marcos, 5–8 km NE of Azogues, 1 Apr. 1945, *Camp E-2490* (NY, UC). CHIMBORAZO: canyon of Río Chanchán near Huigra, 1,200–1,350 m, 7–14 May 1945, *Camp E-2995* (NY), *Camp E-3058* (NY); road Riobamba El Truinfo, between San Juan and Llimbe, 1,700 m, 25 Feb. 1987, *Freire Fierro 598* (AAU); Sibambe, 2,000 m, 28 May 1942, *Haught 3323* (BR mixed coll.). LOJA: road Loja–San Lucas, km 25, 2,200 m, 15 Sep. 1961, *Dodson & Thien 650* (MO, WIS); La Argelia, 2,080 m, 28 Mar. 1946, *Espinosa 14* (NY); W slopes of Cerro Villonaco, 1,800–2,100 m, 9 Apr. 1974, *Harling & Andersson 13302* (GB); Vilcabamba–Yangana road, 1,700–1,800 m, 15 Apr. 1974, *Harling & Andersson 13550* (GB), 1,900 m, 21 Apr. 1980, *Harling & Andersson 18446* (GB); road Loja–Zaruma, between the San Pedro and Las Chinchas, 1,900–2,200 m, 30 Apr. 1974, *Harling & Andersson 14094* (GB); 5 km E of Celica on road to El Empalme, 1,500 m, 11 Apr. 1980, *Harling & Andersson 18181* (GB); road Catamayo (La Toma)–Gonzanamá, ca. 10 km N of Gonzanamá, 2,100 m, 24 Apr. 1980, *Harling & Andersson 18625* (GB); 6 km S of Vilcabamba, 2,100 m, 9 Feb. 1982, *Harling et al. 20454* (GB); between Chuquiribamba and Taquil, 2,200 m, 14 Feb. 1982, *Harling et al. 20719* (GB); 4–6 km N of Yangana on road to Vilcabamba, 1,800–1,900 m, 5 Feb. 1985, *Harling & Andersson 21636* (GB); between Loja and San Lucas, 2,100–2,600 m, 6 Sep. 1923, *Hitchcock 21450* (US); km 66 on Pan American Highway N of Loja, 2,400 m, 3 May 1973, *Holm-Nielsen et al. 4751* (AAU, NY, US); 27–29 km from Porto Velo on road to Loja at the Campamento "Santa Ana," 1,200 m, 22 Feb. 1988, *Molau & Eriksen 3161* (AAU, GB, QCA, QCNE). PERU. AMAZONAS: Prov. Bongara, 11 km E of Pomacocha, 1,950 m, 9 Feb. 1984, *Gentry & Smith 45209* (MO); between Río Utcubamba and Pomacocha, 1,700 m, 29 Jan. 1964, *Hutchison & Wright 3857* (MICH, MO, UC); Prov. Chachapoyas, Tingo, near Chachapoyas, 1,900 m, 12 Apr. 1950, *Ferreyra 7095* (F); W slopes of Cerro Calla-

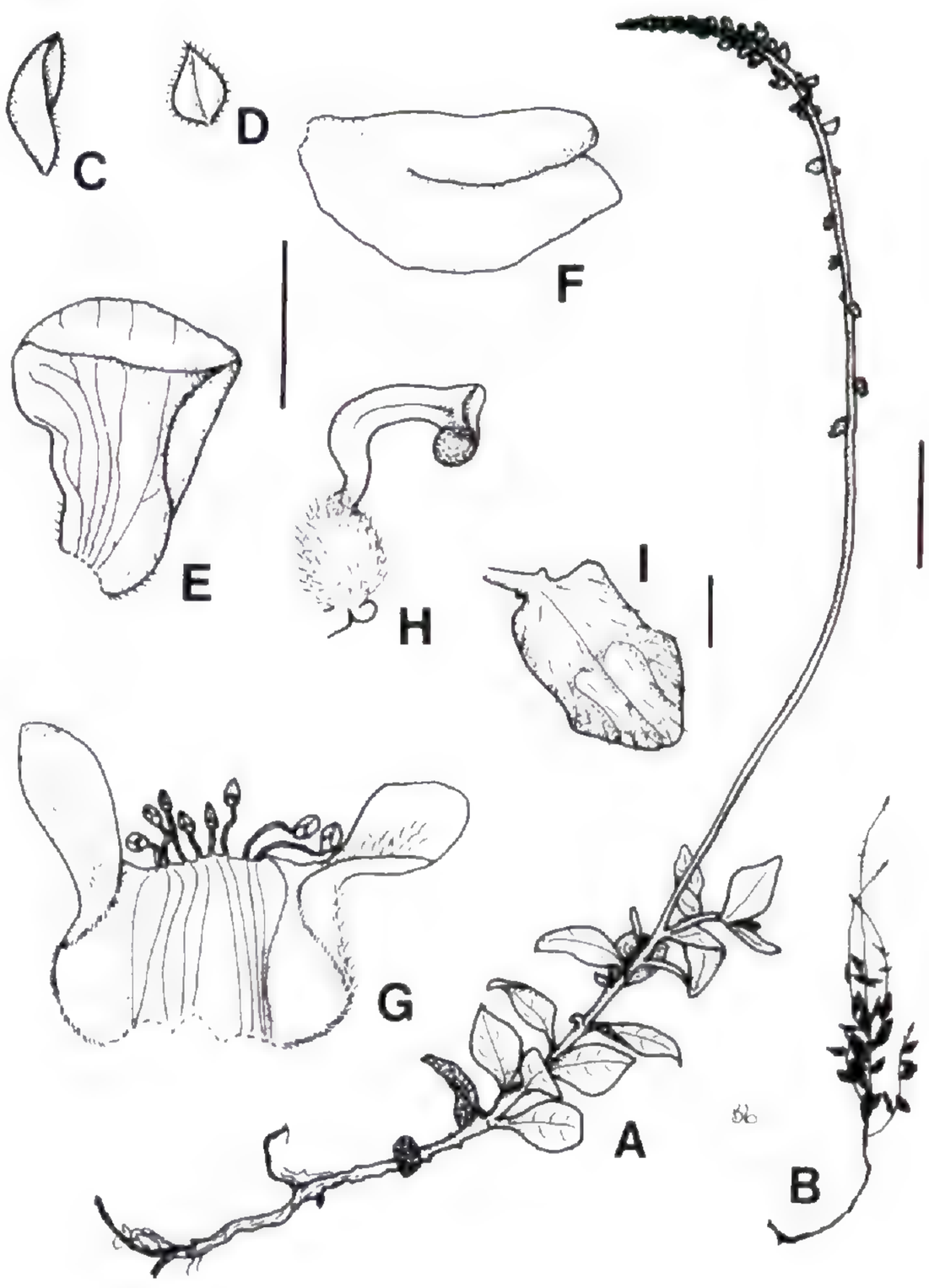


FIGURE 4. *Monnina leptostachya.* —A. Flowering individual. —B. Habit. —C. Upper outer sepal. —D. Lower outer sepal. —E. Wing. —F. Keel. —G. Petal-stamen sheath. —H. Gynoecium. —I. Fruit. A, *Molau, Eriksen et al. 2941* (GB). B I, *Molau & Eriksen 3161* (GB). Scales: A = 3 cm. C–H = 2 mm. I = 1 mm.

Calla, 27 km E of Balsas on road to Leimebamba, 2,250 m, 23 Mar. 1988, *Molau & Eriksen 3385* (GB); Taquia E of Chachapoyas, 2,400–2,500 m, 21 June 1948, *Pennell 15582* (PH); Utcubamba S of Chachapoyas, 1,700–1,750 m, 26 June 1948, *Pennell 15590* (PH); 1 km SW of Chachapoyas, 2,300 m, 22 May 1962, *Wurdack 473* (F, GH, UC, US).

*Monnina leptostachya* is closely allied to *M. polygonoides* but is easily distinguished by its erect habit and blunt anterior stylar lobe (see Fig. 10B and C and discussion under *M. polygonoides*).

Ferreyra (1953) synonymized *M. leptostachya* under *M. herbacea*, based on type photographs and fragments. The two species have, in fact, very little in common, and the mistake would not have been made with the original material at hand.

One record states that the vernacular name is "Guarmiiguila," which means small (female) "Iguila." In Quechua, "Iguila" is the common name for all species of *Monnina*.

**3. Monnina polygonoides** Chodat, Bull. Soc. Bot. Genève sér. 2, 25: 200. 1934. TYPE: Peru. Huánuco: Prov. Huánuco, Ambo, 2,100 m, 5 Apr. 1923, *Macbride 3181* (lectotype,

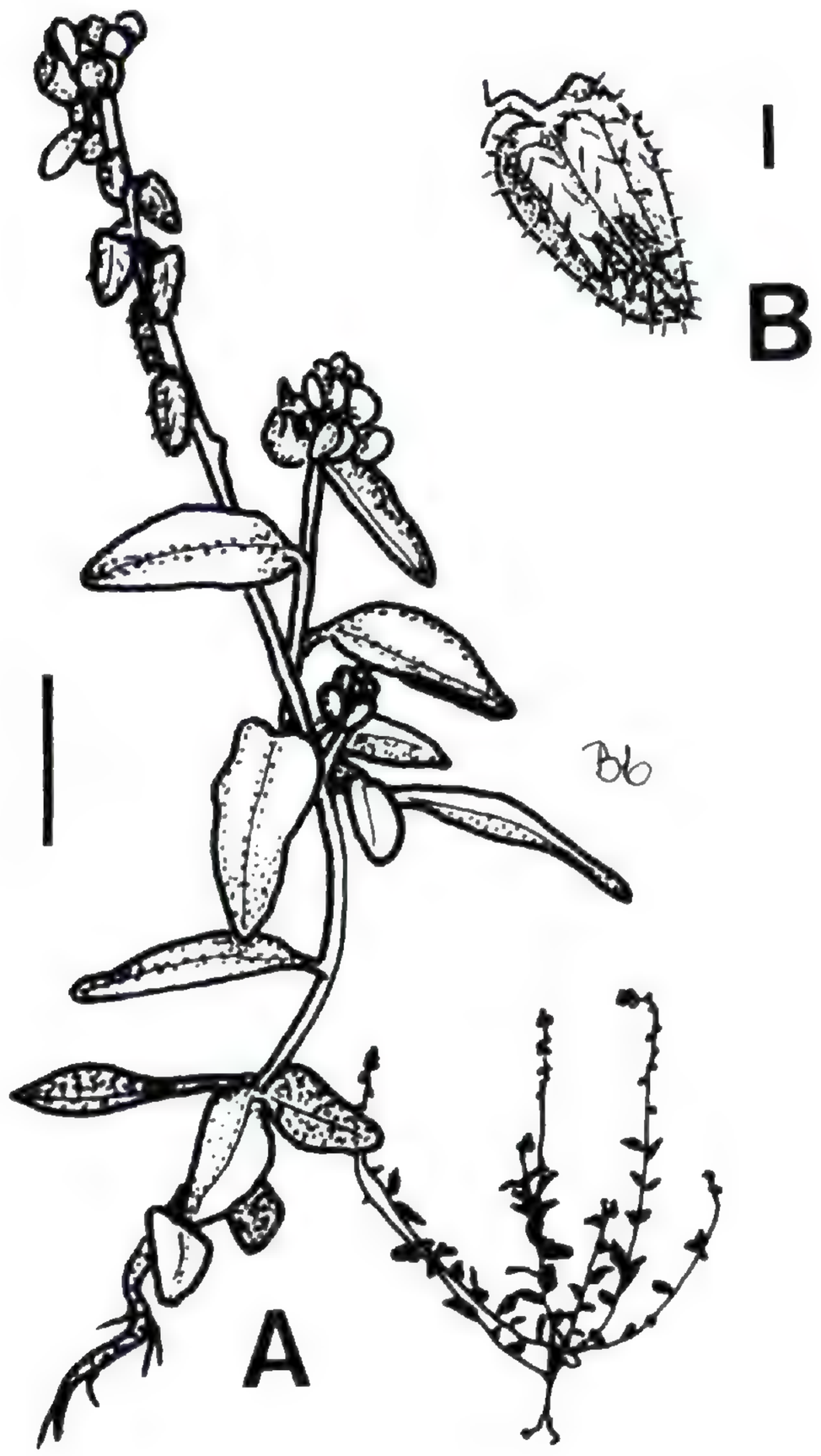


FIGURE 5. *Monnina polygonoides*. —A. Habit and flowering individual. —B. Fruit. A, B, *Molau & Eriksen 3379* (GB). Scales: A = 1 cm. B = 1 mm.

selected by Ferreyra (1946), F; isolectotypes, GH, US). Figure 5.

Annual herb, ascendent, 5–30 cm tall, the branches to 40 cm or more. Stem 0.5–3 mm diam., usually much branched from the base, the stem and branches terete, furrowed by decurrent leaves, white-pubescent, the hairs curved. Leaves exstipulate; petiole 1–1.5 mm long, pubescent; laminae changing in shape and size from base to apex of the branches; lowermost blades narrowly obovate, 0.3–1.5 × 0.1–0.5 cm, obtuse at apex, cuneate at base, middle ones narrowly rhomboid, 0.7–3.2 × 0.3–1.4 cm, acute at apex, cuneate at base, the uppermost leaves lanceolate to linear, 0.9–2.3 × 0.1–0.7 cm, acute at apex, shortly attenuate at base; all laminae chartaceous, minutely mucronate, pubescent on veins and margin, otherwise glabrous (in young leaves pubescent throughout). Inflorescence few-flowered, triangular in outline, 1.5–20(–30) cm; pedicel 0.5 mm; bracts narrowly lanceolate to linear, 1.5 × 0.1–0.2 mm, acute, never exceeding twice the length of the bud, bluish green, ciliate, deciduous. Flowers all chasmogamous; outer sepals usually slightly unequal, the upper one narrowly ovate to lanceolate, 1.5 mm long, 3-nerved, the lower ones ovate, 1.0–1.5 mm long, 1-nerved, all of them ciliate, greenish blue to pale blue; wings obovate, 2.5–3.5 × 2–2.5 mm, truncate at base, glabrous, pale blue; keel 2.5–3.5 × 2 mm, truncate at base, glabrous, pale yellow, 3-dentate at apex; petal-stamen sheath 2.5–3/4–5 mm wide, 1.5–2/2–3 mm long, the petals hirsute adaxially and at base abaxially, the lobes pale blue, otherwise yellowish as the filament sheath; stamens 8, the upper part of filaments free, glabrous, 1–1.5 mm long including the anther, the anther to filament ratio 0.3–0.5; style 1.5–2 mm long, glabrous, bent 45° just above the middle; anterior stylar lobe a pointed tooth, 0.2–0.25 mm long, the posterior lobe with a sessile, rounded stigma (Fig. 10C). Fruit 2-locular, narrowly obpyriform with a dorsal gibba, 2 × 4 mm, villous, wingless, green, the gibba purple.

*Distribution.* Northern to central Peru. Steep, rocky slopes in dry, mountainous areas, 2,000–2,850 m (Fig. 6C). It has been collected flowering from February to May, i.e., from the end of the rainy season and a couple of months onward.

*Specimens examined.* PERU. AMAZONAS: Prov. Bongara, road Moyobamba–Chachapoyas, 2,250 m, 13 Apr. 1984, *Croat 58232* (MO); Prov. Chachapoyas, 9 km below and W of Chachapoyas on road to Caclic, 2,000 m, 25 Mar. 1964, *Hutchison & Bennett 4516* (F, UC). ANCASH: Prov. Bolognesi, Conay, 6 km below Chiquián, 2,600 m, 12 May 1950, *Ferreyra 7381* (UC, mixed coll.); Prov. Huaylas, dry hillsides above Río Santo across from Mancos, 10 Apr. 1970, *Earle Smith & Blas 4922* (US). CAJAMARCA: Prov. Cajamarca, Quebrada de San Vicente SW of Cajamarca, 2,800–2,850 m, 4 Apr. 1948, *Pennell & Reichlin 14999* (PH); Prov. Celendín, Celendín, 2,700 m, 18 May 1964, *Hutchison & Wright 5144* (F, GH, MICH, MO, UC); 4–5 km E of Celendín on road to Balsas, 2,750 m, 23 Mar. 1988, *Molau & Eriksen 3379* (GB); Limón E of Celendín, 2,000 m, 15 Apr. 1948, *Pennell 15181* (GH, PH). HUANUCO: Prov. Ambo, Puente Huandobamba, 2,240 m, 8 Feb. 1982, *Ochoa 14551* (F, US); Prov. Huánuco, Acomayo, 2,100 m, 10 Feb. 1946, *Woytkowski 34014* (F, MO, UC), 2,300 m, 22 Apr. 1946, *Woytkowski 34234* (F, MO, UC). LA LIBERTAD: Prov. Santiago de Chuco, near Santiago de Chuco, 2,800 m, 13 June 1984, *Sagástegui et al. 11773* (MO). PASCO: Prov. Pasco, Huariaca, 2,900 m, 3 Apr. 1923, *Macbride 3116* (syntypes, GH, MICH, US). Department unknown: sine loco, *Weberbauer 6235* (F).

*Monnina polygonoides* is closely related to *M. leptostachya*. These two species are primarily characterized by 2-locular, villous fruits. However, *Monnina polygonoides* is ascendent, has pale blue flowers, and a pointed anterior stylar lobe (Fig.

10C), whereas *M. leptostachya* is erect, has dark blue flowers, and a blunt anterior stylar lobe. The two species may be confused when dried, but they are easily distinguished in the field because of habit and flower color.

Ferreyra (1946) synonymized *M. polygonoides* under *M. herbacea* and thereby also related it to *M. leptostachya* (see above under this species). *Monnina polygonoides* is, as mentioned above, closely related to *M. leptostachya*, but it has little in common with *M. herbacea*.

**4. Monnina ramosa** I. M. Johnston, Contr. Gray Herb. 70: 77. 1924. TYPE: Peru. Arequipa: Prov. Arequipa, S slope of Chachani Mountain N of Arequipa, 3,355 m, Mar. 1920, *Hinkley & Hinkley 13* (holotype, GH; isotype, US).

Perennial herb, 15–25 cm tall. Stem 1.5–2.5 mm diam., terete, much branched from the base, the branches spreading, white-pubescent, the hairs curved. Leaves exstipulate; petiole 0.5–1 mm long, pubescent; blade lorate to linear, 8–30 × 1–2 mm, chartaceous, acute at apex, cuneate at base, white-pubescent throughout. Inflorescence many-flowered, narrowly triangular to very narrowly triangular in outline, 5–18 cm long; pedicel 0.5 mm; bracts narrowly ovate to ovate, acute 1.2–2 × 0.7–1 mm, bluish, pilose. Flowers all chasmogamous; outer sepals ± equal, narrowly to broadly ovate, 1.2–2.0 × 0.6–1.0 mm, bluish, ciliate; wings obovate, 3.5 × 2 mm, cuneate at base, blue, glabrous; keel 3 × 1.5–2.5 mm, truncate at base, yellow at least apically, glabrous, 3-lobed at apex, the central lobe emarginate; petal-stamen sheath 1.5–2/3.5 mm wide, 2/3 mm tall, hirsute adaxially at sinus between the petal lobe and the staminal sheath and sparsely on the lower half of the petal; stamens 8, the upper part of the filaments free, glabrous, 1 mm long including the anther, the anther to filament ratio 1.0; style 1.5 mm long, glabrous, bent 80° ⅔ from base; anterior stylar lobe a long (0.2 mm), pointed tooth, the posterior lobe a 0.5-mm-long stalk with a rounded stigma at the tip (Fig. 10D). Fruit unilocular, compresed, ± elliptic, 4 × 3 mm, densely strigose with a glabrous wing.

*Distribution.* Only known from southernmost Peru, where it occurs in sandy habitats above 2,300 m (Fig. 6E). It may be endemic to the Arequipa area or it may be present further south reaching into the adjacent mountains of northern Chile (although it has not yet been collected there).

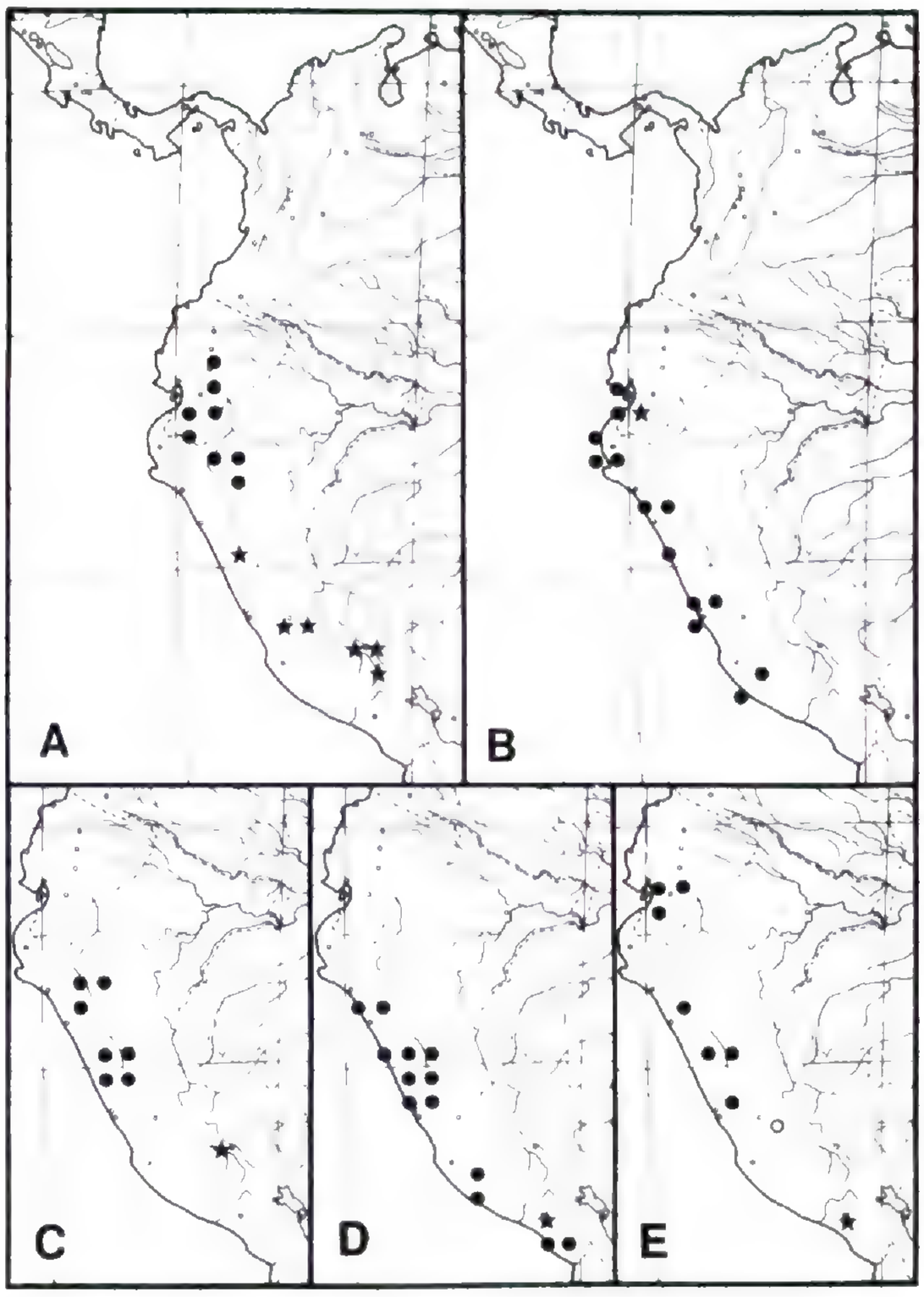


FIGURE 6. Distributions of the species of *Monnina* subg. *Pterocarya* in northwestern South America. —A. *Monnina leptostachya* (dots) and *M. amarella* (stars). —B. *Monnina fosbergii* (star) and *M. pterocarpa* (dots). —C. *Monnina polygonoides* (dots) and *M. wrightii* (star). —D. *Monnina macrostachya* (dots) and *M. macbridei* (star). —E. *Monnina herbacea* (dots), *M. ramosa* (star), and *M. filifolia* (circle).

*Specimen examined.* PERU. AREQUIPA: Prov. Arequipa, Volcán Misti, 2,300 m, July–Aug. 1921, *Rutten 1019* (U).

*Monnina ramosa* has, like *M. fosbergii* from Ecuador, a general appearance similar to that of *M. linearifolia* from Chile, i.e., a decumbent, woody perennial with small, linear leaves. The most obvious distinction between *M. linearifolia* and *M. ramosa* is that the former has six stamens not eight. *Monnina fosbergii*, like *M. ramosa*, has eight stamens with the upper part of the filaments free, but all other flower parts are different. The fruit of *M. fosbergii* is 2-locular while that of *M. ramosa* is 1-locular. *Monnina ramosa* grows sympatrically with *M. macbridei*, but the latter species is easily recognized because it is annual and has seemingly sessile anthers.

The exact colors of the flower parts are uncertain. The colors fade in the drying process, and the label data are imperfect.

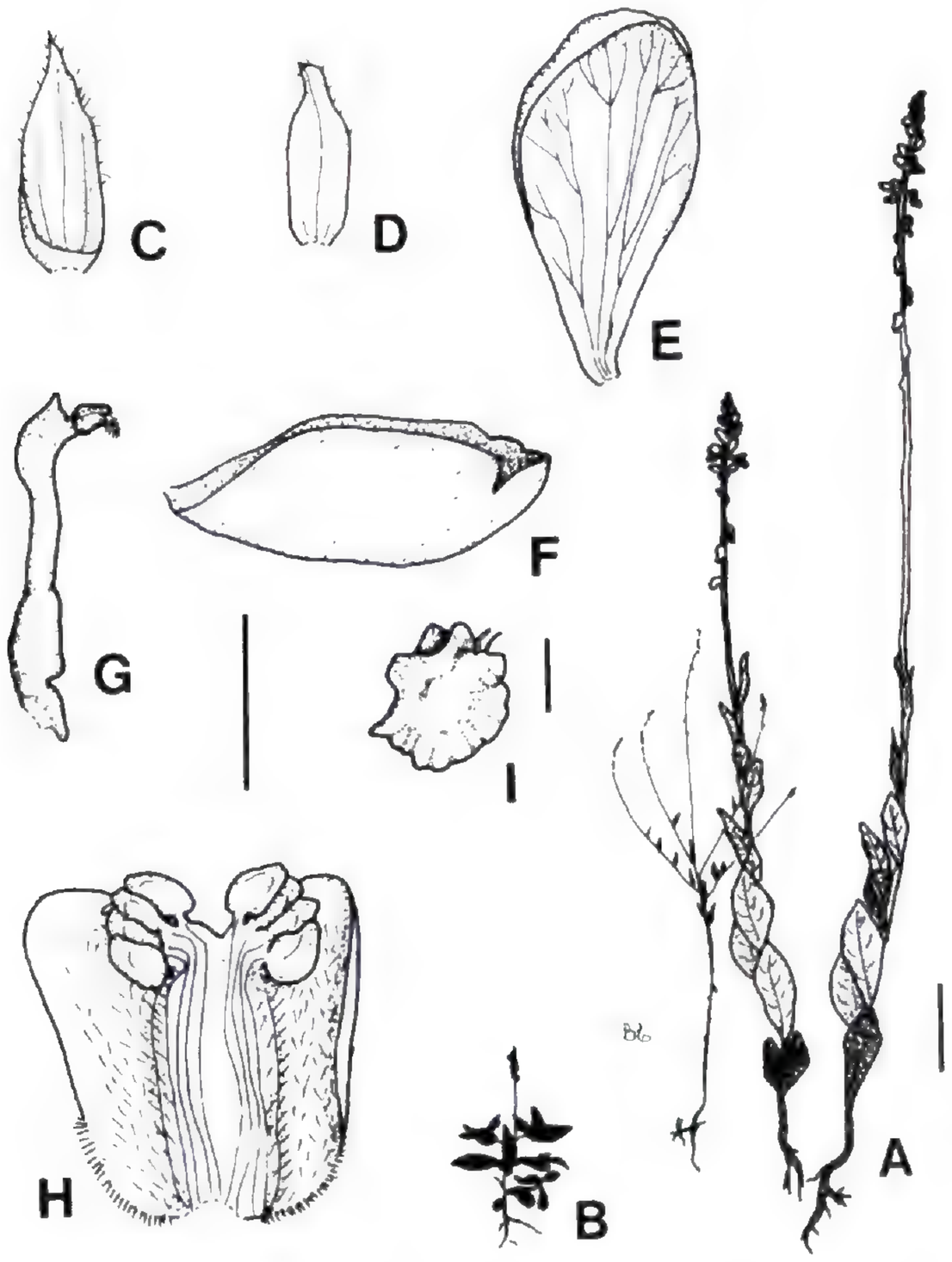


FIGURE 7. *Monnina macrostachya*. —A. Habit and flowering individuals. —B. Habit of Loma type. —C. Upper outer sepal. —D. Lower outer sepal. —E. Wing. —F. Keel. —G. Gynoecium. —H. Petal-stamen sheath. —I. Fruit. A, C–I, *Molau & Eriksen 3515* (GB). B, *Grant 7440* (GH). Scales: A = 2 cm. C–H = 1 mm. I = 1 mm.

**5. Monnina macbridei** Chodat, Bull. Soc. Bot. Genève sér. 2, 25: 199. 1934. TYPE: Peru. Arequipa: Prov. Arequipa, Arequipa, 2,500–2,600 m, 7–16 Apr. 1925, *Pennell 13167* (lectotype, selected by Ferreyra (1946), F; fragments, USM; isolectotypes, GH, LE, NY, PH, S, US).

Annual herb, 5–35 cm tall. Stem erect, 0.5–2 mm diam., terete or slightly furrowed by decurrent leaves, unbranched or sparsely branched distally, white-pubescent, the hairs curved. Leaves exstipulate; petiole 0.5–1 mm long, pubescent; laminae on the main axis changing in shape and size from base to apex of the stem; lowermost blades spathulate, 1.4–3.0 × 0.2–0.5 cm, upper ones lorate to linear, 1.7–4.2 × <0.1–0.4 mm, acute at apex, cuneate at base; all laminae chartaceous, white-pubescent throughout. Inflorescence many-flowered, very narrowly triangular in outline, 2–25 cm long; pedicel 0.5 mm long; bracts lanceolate, 1.5–2.0 × 0.5 mm, acuminate, probably green with bluish tinge, glabrous. Flowers all chasmogamous; outer sepals unequal in shape and size, pale blue, glabrous; the upper sepal narrowly ovate, 1.5 × 0.7 mm, the lower ones narrowly ovate to lanceolate, 1.0–1.5 × 0.5 mm, all acute at apex; wings obovate to narrowly obovate, 1.5–2 × 3 mm, cuneate at base, pale blue, glabrous; keel 1.5 × 2.5–3.5 mm, cuneate at base, glabrous, profoundly emarginate and 2-lobed at apex, probably yellow throughout; petal-stamen sheath 1–2/2–3 mm wide, 2–2.5 × 2.5–4 mm tall, the petal sheath hirsute adaxially, the lobes probably pale blue, otherwise greenish yellow as the filament sheath; stamens 8, the anther 0.1–0.2 mm long, seemingly sessile or the two central anthers occasionally with a 0.1-mm-long free filament; style 1–1.5 mm long, glabrous, straight or bent 30° ⅔ up; anterior stylar lobe an upright pointed tooth, 0.1 mm long, the posterior lobe a 0.4–0.6-mm-long stalk, bent 90° in relation to the style, with a rounded stigma at the tip (Fig. 10E). Fruit unilocular, broadly elliptic to circular in outline, 3–4 × 3–4 mm, glabrous or pubescent, winged, green, possibly purple-spotted.

*Distribution.* From the present collections, *M. macbridei* seems endemic to the Arequipa area in southern Peru, where it inhabits sandy sites on dry slopes, ca. 2,000–3,400 m (Fig. 6D). As argued earlier under *M. ramosa*, which occurs sympatrically with this species, it is plausible that the distribution extends into the mountains of northern Chile.

*Specimens examined.* PERU. AREQUIPA: Prov. Arequipa, Arequipa, 21 Aug. 1925, *Cockerell s.n.* (US); Chachani mountains N of Arequipa, 3,355 m, Mar. 1920, *Hinkley & Hinkley 18* (GH); Tingo, 2,100–2,300 m, 8 Apr. 1925, *Pennell 13110* (syntypes of *M. macbridei*, GH, LE, US); SW side of Río Chili, 4 km N of Arequipa, 2,500 m, 8 May 1977, *Solomon 2780* (MO).

*Monnina macbridei* is close to *M. macrostachya* in some aspects. Both have a petal-stamen sheath with eight seemingly sessile anthers, a character that is unique for these two species. The habit of *M. macbridei* is very similar to that of *M. macrostachya*. The two species differ in other characters, e.g., the posterior stylar lobe, the stigma, and the apex of the keel.

**6. Monnina macrostachya** Ruíz & Pavón, Syst. Veg. Fl. Peruv. Chil. 1: 173. 1798. TYPE: Peru. Lima: Provinces of Cercado (Lima) and Chancay, *Ruíz & Pavón s.n.* (lectotype, selected here, MA). Figure 7.

*Monnina lanceolata* (Poir.) DC., Prodr. 1: 339. 1824. Basionym: *Polygala lanceolata* Poir., Encycl. 5: 498. 1804. TYPE: Peru. Sine loco, *Jussieu s.n.* (holotype, P).

*Monnina macrostachya* var. *pumila* A. Gray, U.S. Exploring Expedition 15, Botany, Phanerogamia part I: 107. 1854. TYPE: Peru. Lima: Prov. Canta, above Obrajillo, *Wilkes expedition s.n.* (lectotype, selected here, GH; isolectotype, US).

*Monnina weberbaueri* Chodat, Bot. Jahrb. Syst. 42: 102. 1909. TYPE: Peru. Arequipa: Prov. Islay, Mollendo, 20–100 m, 1906, *Weberbauer 1505* (lectotype, selected here, G).

*Monnina weberbaueri* var. *elongata* Chodat, Bot. Jahrb. Syst. 42: 102. 1909. TYPE: Peru. Ancash: Prov. Cajatambo, below Ocros, 2,300–2,400 m, *Weberbauer 2724* (B probably destroyed). NEOTYPE: Peru. Ancash: Prov. Bolognesi, between Colcas and Cajacay, 2,400 m, 8 Apr. 1988, *Molau & Eriksen 3515* (GB).

*Monnina weberbaueri* var. *pachyantha* Chodat, Bot. Jahrb. Syst. 42: 102. 1909. TYPE: Peru. Lima: Prov. Huarochiri, railroad between Lima and Oroya, near Matucana, 3,000 m, *Weberbauer 185* (B probably destroyed). NEOTYPE: Peru. Lima: Prov. Huarochiri, Matucana, 2,900 m, 9 Apr. 1939, *Goodspeed 11332* (GH; isoneotypes, NA, UC).

*Monnina weberbaueri* var. *maxima* Chodat, Bot. Jahrb. Syst. 42: 102. 1909. TYPE: Peru. Ancash: Prov. Huaylas, between Samanco and Caraz, 3,100 m, *Weberbauer 3125* (lectotype, selected here, MOL).

*Monnina arenicola* Ferreyra, J. Arnold Arbor. 27: 137. 1946. TYPE: Peru. Arequipa: Prov. Islay, S of Mollendo, 17 Nov. 1935, *Mexia 4175* (holotype, GH; fragments, USM; isotypes, M, UC).

Annual herb, 3.5–46 cm tall. Stem erect, 0.5–3 mm diam., terete, slightly furrowed by decurrent leaves, unbranched to much branched all along the main axis, the branches erect or ascending, white-pubescent, the hairs curved. Leaves exstipulate; petiole 1–2 mm long, pubescent; laminae on the main axis changing in shape from base to apex of the stem; lowermost blades narrowly obovate, 0.4–3.6 × 0.2–1.8 cm, obtuse to acute at apex, middle ones narrowly rhomboid, 1.0–4.2 × 0.4–2.1 cm, acute at apex, and uppermost blades lanceolate to linear, 0.8–4.2 × 0.1–1.2 cm, acute at apex; all laminae chartaceous, minutely mucronate, cuneate at base, pubescent on veins, margin, and sometimes the upper surface, otherwise glabrous (in young leaves pubescent throughout). Inflorescence many-flowered, 1.5–31 cm long, dense at apex, rather abruptly becoming looser and more expanded; pedicel 1 mm long; bracts lanceolate, acuminate, 1.0–2.0 mm long, ciliate, blue. Flowers all chasmogamous; outer sepals usually unequal in shape and size, blue; upper sepal ovate to narrowly ovate, 1.5–3 mm long, boat-shaped, acuminate, glabrous or ciliate along margin and midrib abaxially, lower sepals narrowly ovate to lanceolate, 1–2.5 mm long, acuminate, glabrous or ciliate along the margin; wings obovate, 1.5–3 × 3–4.5 mm, cuneate at base, glabrous or ciliate basally along the abaxial margin, blue; keel 1.5–2 × 3–5 mm, 3-dentate at apex, cuneate and ciliate at base, usually sparsely pilose along the midrib adaxially, blue, the apex or only the central tooth yellow; petal-stamen sheath 1.5–3/3–5 mm wide, 2–4.5/2.5–5 mm long, the petals hirsute adaxially and at least at base abaxially, the lobes blue, otherwise greenish as the filament sheath; stamens 8, the anther 0.2–0.7 mm long, seemingly sessile; style 1.5–3 mm long, glabrous, bent 80–90°, rarely less, ca. ⅓ from apex; anterior stylar lobe a short (ca. 0.1 mm) pointed tooth, the posterior lobe 0.5–0.8 mm long, at base carrying a bilobed, discoid stigma, the apex a pointed, hirsute tooth (Fig. 10F). Fruit unilocular, 2 × 2 mm, glabrous or pubescent, in dry condition lacunate, usually winged but often irregularly so, green, often suffused with purple.

Reddish flowers occur in some specimens. In the population I saw, ca. 10% of the individuals had red flowers.

*Distribution.* Peru. In sand dunes and in Lomas near the coast or on rocky slopes in the mountains, 0–3,500 m (Fig. 6D).

*Specimens examined.* PERU. ANCASH: Prov. Bolognesi, Chacchash, near Chiquián, 3,220 m, 12 Apr. 1949, *Ferreyra 5681* (US); Casca, below Chiquián, 3,100–3,200 m, 28 Apr. 1950, *Ferreyra 7316* (US); Conay, 6 km below Chiquián, 2,600 m, 12 May 1950, *Ferreyra 7381* (UC, mixed coll.); below Chiquián, 3,200–3,300 m, 22 May 1948, *Pennell 15412, 15413* (PH); Prov. Carhuaz, N of Chancos, 3,000–3,100 m, 11 May 1948, *Pennell 15314* (PH); Prov. Huaylas, trail to cave across Río Santo from Mancos, 9 Apr. 1970, *Earle Smith & Blas 4902* (US, mixed coll.). AREQUIPA: Prov. Caraveli, N of Pta. Chala, 18 Aug. 1957, *Ellenberg 2648* (U); Prov. Islay, 6 km E of Matarani, 580 m, 17 Nov. 1986, *Dillon et al. 4830* (US); 7 km NE of Matarani, 350 m, 22 Dec. 1974, *Evaristo López 51* (MO); Mollendo, 16 Oct. 1925, *Johnston 3551* (GH), 600 m, 6 July 1946, *Pearson & Pearson 25* (PH), 175 m, 30 Sep. 1938, *Worth & Morrison 15762* (GH, UC, US). AYACUCHO: Prov. Lucanas, between Nazca and Puquio, 1,500–1,600 m, 19 Mar. 1949, *Ferreyra 5452* (F). CAJAMARCA: Prov. Contumazá, La Herilla, Guzmango, 3,300 m, 19 Apr. 1967, *Sagástegui et al. 6426* (GH, MO, US); El Granero, 2,800 m, 14 June 1983, *Sagástegui & López 10657* (MO, US); around Guzmango, 2,500 m, 22 May 1978, *Sagástegui & Mostacero 9100* (F, MO); 2,300 m, 29 Apr. 1982, *Sagástegui et al. 10331* (MO). HUANUCO: Prov. Huánuco, Mito, ca. 2,750 m, 8–22 July 1922, *Macbride & Featherstone 1548* (F). LA LIBERTAD: Prov. Otuzco, Salpo–Chanchacap, 2,800 m, 24 May 1984, *Sagástegui et al. 11653* (MO, US). LIMA: Prov. Cajatambo, Ambar, 2,010 m, 16 Apr. 1939, *Stork 11451* (GH, UC); Prov. Canta, near Yaso on the Lima–Canta road, 1,600–1,800 m, 8 May 1950, *Ferreyra 7256* (US); summit between Huamantanga and Puruchuco, *Matthews 461* (GH); Canta, 2,700–2,900 m, 11–19 June 1925, *Pennell 14343* (F, GH, PH); along Río Chillón, above Obrajillo, 2,700 3,000 m, 13–23 June 1925, *Pennell 14372* (F, GH, PH), *14373* (PH), 2,300–2,400 m, 15–17 June 1925, *Pennell 14436* (F, GH, LE, PH);

Prov. Chancay, Lomas de Pasamayo, S of Chancay, 300 m, 4 Oct. 1938, *Stork & Vargas 9351* (GH, MO, NA, UC); Prov. Huarochiri, Matucana, 2,100 m, 27 May 1950, *Ferreyra 7598* (UC), 2,450 m, 12 Apr.–3 May 1922, *Macbride & Featherstone 88, 311* (F), 2,400 m, 18 Feb. 1954, *Rauh & Hirsch P191* (F), 2,500 m, 11 Sep. 1938, *Stork & Horton 9143* (GH, UC); Río Blanco, 3,500 m, 25 Mar. 1952, *Hutchison 567* (UC); above Sta. Eulalia, 1,300 m, 3 Mar. 1942, *Goodspeed 33016* (UC); Prov. Lima, S of Lima, 31 July 1941, *Grant 7440* (GH, MICH, MO, UC, US); 70 km E of Lima, just W of Surco, 1,700 m, 24 Mar. 1952, *Hutchison 553* (UC); Surco, 2,034 m, Feb. 1948, *Soukup 3722* (F). MOQUEGUA: Prov. Ilo, 9 km E of Ilo, 250 m, 20 Aug. 1957, *Ellenberg 2732* (U); Prov. Moquegua, Carumas, 3,200 m, 21 Feb.–6 Mar. 1925, *Weberbauer 7301* (F); Mt. Estuquiña, NW of Moquegua, 2,000–2,100 m, Mar. 1925, *Weberbauer 7451* (F, GH, US, WIS). PASCO: Prov. Daniel Carrión, Yanahuanca, ca. 3,050 m, 16–22 June 1922, *Macbride & Featherstone 1168* (F). Department and Province unknown: sine loco, *Fischer s.n.* (LE).

In his systematic overview of the genus *Monnina*, Chodat (1896) classified *M. macrostachya* among the stipulate species. In 1909, he described the taxon *M. weberbaueri* and its three varieties to accommodate some exstipulate specimens from central and southern Peru, otherwise essentially like *M. macrostachya*. The type of *M. macrostachya* is, however, exstipulate, and thus I have here synonymized *M. weberbaueri* and its varieties under *M. macrostachya*.

*Monnina macrostachya* is a very variable species. In Lomas and sand dunes, the plants are often lower than they are when growing in the mountains, but the leaves are not proportionally smaller, which results in a very peculiar appearance (Fig. 7B). *Monnina arenicola* and *M. macrostachya* var. *pumila* were described mainly on the basis of smaller plant size, but I have found no evidence in other characters supporting the exclusion of small plants into a separate taxon. The degree of reduction of the fruit wing varies considerably. There is a continuous series of forms—from fruits with entire wings through very irregularly winged ones to completely wingless fruits. Furthermore, the fruits range from glabrous to densely pubescent.

**7. Monnina amarella** Chodat, Bull. Soc. Bot. Genève sér. 2, 25: 200. 1934. TYPE: Peru. Cuzco: Prov. Cuzco, San Sebastián, 3,300–3,400 m, 25 Apr. 1925, *Pennell 13629* (lectotype, selected by Ferreyra (1946), F; isolectotypes, GH, NY, PH, US). Figure 8D–F.

Annual herb, 3–27 cm tall. Stem erect, 0.5–2 mm diam., terete, furrowed by decurrent leaves, usually branched all along the main axis, the branches erect, white-pubescent, the hairs curved. Leaves exstipulate; petiole 0.5–1 mm long; laminae on the main axis changing in shape and size from base to apex of the stem, the basal ones oblanceolate, 0.5–1.6 × 0.2–0.6 cm, obtuse and emarginate at apex, the upper ones narrowly lanceolate to linear, 0.8–3.7 × 0.1–0.9 cm, obtuse and either minutely mucronate or rarely emarginate or acute at apex; all laminae chartaceous, cuneate to attenuate at base, glabrous except on the midrib. Inflorescence few-flowered, "torpedo"-shaped in outline, 1.5–18 cm long; pedicel 0.5 mm long; bracts lanceolate to narrowly lanceolate, acuminate, ca. 0.5–1.5 mm long, dark blue, glabrous. Flowers of the main inflorescence chasmogamous, those of the branches usually cleistogamous (measurements for these given in parentheses); outer sepals unequal in shape and size, dark blue, glabrous; upper sepal ovate to narrowly ovate, 1.3–1.5 × 0.6–1.0 mm (0.8–1.5 × 0.6–1.0 mm), boat-shaped, acute, lower sepals narrowly ovate to lanceolate, 1.0–1.2 × 0.3–0.5 mm (0.8–1.0 × 0.3 mm); wings narrowly obovate, 2–2.5 × 1–1.5 mm (2–2.5 × 1–1.5 mm), cuneate at base, glabrous, dark blue; keel 2.5 × 1.5 mm (2–2.5 × 1–1.5 mm), 3-lobed at apex, the central lobe emarginate, truncate at base, glabrous, yellow; petal-stamen sheath 1.5–2.5/4–4.5 mm (1–2/3–4 mm) wide, 1–2/1–2.5 mm (1–2 × 1–2 mm) long, the petals pilose to hirsute adaxially on sheath, the lobes dark blue, otherwise greenish like the filament sheath; stamens 6, in flowers on branches often 4, the filaments of the 3 (2) anthers of each fascicle fused throughout (Fig. 8F), glabrous, 0.8–1 mm (0.8–1.0 mm) including the anthers, the anther to filament ratio 0.25–0.5 (0.3); style 1.5–2.0 mm (1–1.5 mm) long, glabrous, evenly curved, the central part dorsiventrally expanded building a cavity, to 0.8 mm wide; anterior stylar lobe a short pointed tooth, 0.1–0.2 mm long, the posterior lobe with a sessile, rounded stigma (Fig. 10G). Fruit 1-locular, compressed, rotund in outline, 2.5–4.5 × 3.5–5 mm when mature, glabrous or puberulent, green, often partly covered by the remaining, withered keel, the wing ca. 0.8 mm wide, bluish-tinged.

*Distribution.* Central and southeastern Peru. Open slopes among grass and rocks in the mountains, ca. 2,000–4,000 m (Fig. 6A).

*Specimens examined.* PERU. ANCASH: Prov. Huaraz, Cerro Shaurema SE of Huaraz, 3,250 m, 9–13 May 1948, *Pennell 15357* (PH). AYACUCHO: sine loco, ca. 2,400 m, 1951, *Soukup 4018* (F). CUZCO: Prov. Acomayo, vicinity of Acomayo, 3,200 m, Feb. 1937, *Vargas 491* (F); Prov. Anta, Huaypo Grande, Huanacori, 3,720 m, 2 Apr. 1973, *Brunel 667* (F, GH); Huanacori, 3,750 m, 18 Apr. 1973, *Brunel 906* (MO); Pampa de Anta,

vicinity of Huarocondo, 3,200 m, *Herrera 3638* (F); Prov. Canchis, Checacupe, 3,400 m, 5 Apr. 1954, *Rauh & Hirsch P707* (F); Prov. Calca, Intihuatana Pisac, 3,300 m, 20 Mar. 1945, *Vargas 5061* (MO); Prov. Cuzco, Collutaro, ESE of Cuzco, 3,400 m, 14 Apr. 1957, *Ellenberg 1029* (U); near Cuzco, 3,300–3,500 m, Apr. 1925, *Herrera 681* (F, US syntype), 3,600 m, Mar. 1929, *Herrera 2393* (F); road between Cuzco and Urcos, km 34 at Huaro, 3,100 m, 25 May 1977, *Solomon 3086* (MO); E of Cuzco on road to Pisac, 3,700–3,900 m, 11 Apr. 1985, *Stein et al. 2532A* (MO); Saxaihuaman, 3,600 m, Mar. 1929, *Herrera 2388* (syntype, F), 3,500–3,600 m, 24 Apr. 1925, *Pennell 13589* (PH); Prov. Urubamba, Machupicchu, 2,000 m, 10 Apr. 1957, *Ellenberg 1184* (U); Chincheros, 3,000–3,300 m, 16 Feb. 1982, *King et al. 300* (ECON, F); Ollantaytambo, 3,000–3,100 m, 26 Apr. 1925, *Pennell 13678* (PH), 3,100 m, 22 Apr. 1982, *Peyton & Tilney Peyton 33* (MO); Chicon Canyon, 2,900–3,200 m, 7 Mar. 1939, *Vargas 11061* (F, UC). HUANCAVELICA: Prov. Huancavelica, 8 km E of Mejorada, 2,400 m, 13 Mar. 1939, *Stork & Horton 10909* (F, UC); vicinity of Mejorada, 2,800–2,820 m, 24 Mar. 1951, *Tovar 295* (US). JUNIN: Prov. Huancayo, Huancayo, Mar. 1946, *Soukup 2950* (F, GH, MO), 3,270–3,300 m, 1 Apr. 1951, *Tovar 331* (US).

*Monnina amarella* possesses two kinds of flowers: normal chasmogamous flowers with six stamens on the main inflorescence, and smaller, cleistogamous flowers with four stamens and more or less reduced petal-stamen sheath on the branches. Cleistogamous flowers are found in *M. wrightii* as well.

Vernacular name: "bolsa bolsa."

**8. Monnina filifolia** Chodat, Bull. Soc. Bot. Genève sér. 2, 25: 198. 1934. TYPE: Peru. Huancavelica: Prov. Tayacaja, valley of the Mantaro River, below Colcabamba, 1,900 m, Mar. 1913, *Weberbauer 6454* (holotype, F: isotypes, GH, NY, S, US, USM).

Annual herb, 43–65 cm tall. Stem erect, 1.5–3 mm diam., terete, furrowed by decurrent leaves, unbranched or branched distally, the branches erect, white-pubescent, the hairs curved. Leaves exstipulate; petiole 1–2 mm long; laminae changing in shape and size from base to apex of the stem, the basal ones oblanceolate, 1.3–1.9 × 0.2–0.3 cm, obtuse or sometimes obtuse with a point at apex, the upper ones linear, 2.5–7.0 × 0.1–0.3 cm, acute at apex; all laminae chartaceous, cuneate at base, glabrous. Inflorescence many-flowered, very narrowly triangular in outline, 21–46 cm long; pedicel 1 mm long; bracts linear, acute, ca. 2 mm long, glabrous. Flowers all chasmogamous; outer sepals unequal in size, narrowly ovate, ciliate; upper sepal 1.5 × 0.8 mm, boat-shaped, the lower ones 1.0 × 0.5 mm; wings obovate, 2.5 × 1.5 mm, cuneate at base, glabrous, lilac (fide Weberbauer); keel 2.5 × 1 mm, 3-lobed at apex, the central lobe deeply emarginate, truncate at base, glabrous, yellow (fide Weberbauer); petal-stamen sheath 1.5/3 mm wide, 1/1.5 mm long, the petals hirsute adaxially at base, the lobes lilac (fide Weberbauer); stamens 6, the filaments of the three stamens in each fascicle fused throughout, glabrous, 0.8 mm long, the anther to filament ratio 1.0; style 1 mm long, glabrous, evenly curved, the central part diventrally expanded building a cavity; anterior stylar lobe a short blunt tooth, the posterior lobe with a sessile, elongate stigma (Fig. 10G). Fruit 1-locular compressed, rotund in outline, 5 × 4 mm when mature, densely pubescent, the wing ca. 0.8 mm wide.

*Distribution.* Central Peru, ca. 2,000 m (Fig. 6E). Known only from the type collection.

*Monnina filifolia* is very similar to *M. amarella*. Both lack stipules and have six anthers with the three filaments of each fascicle united throughout. The most striking differences between the two species are the growth habit (branches only developed distally vs. all along the main axis), the leaf size and shape (upper leaves very long, narrow, and acute vs. shorter, wider, and obtuse), the number of flowers (many vs. few), and the outline of the inflorescence (very narrowly triangular vs. "torpedo"-shaped). The leaf size and shape vary within many other species, whereas growth habit, flower number, and inflorescence outline are generally constant characters within a species. The collection of *M. filifolia* comes from a lower altitude (1,900 m) than the majority of the *M. amarella* collections (2,900–3,900 m). That fact indicates either that *M. filifolia* is a separate taxon with a distinct habitat preference, or that *M. filifolia* should be lumped into *M. amarella* as a lowland ecotype. It is important to note that *M. amarella* collections from approximately the same geographical area and comparatively low altitude as *M. filifolia* (*Stork & Horton 10909* and *Soukup 4018*, both 2,400 m) have a tendency toward longer and more narrow leaves. However, more ample material is needed to determine whether *M. filifolia* should be considered a separate taxon, as done here, or whether it should be included in *M. amarella*.

**9. Monnina wrightii** A. Gray, Pl. Wright. 2: 31. 1853. TYPE: U.S.A. New Mexico: near the copper mines, 1851, *Wright 938* (lectotype, selected here, GH; isolectotypes, GH, NY, PH, US). Figure 8A–C.

*Monnina brachystachya* Griseb., Abh. Königl. Ges. Wiss. Göttingen 19: 75. 1874. TYPE: Argentina. Tucu-

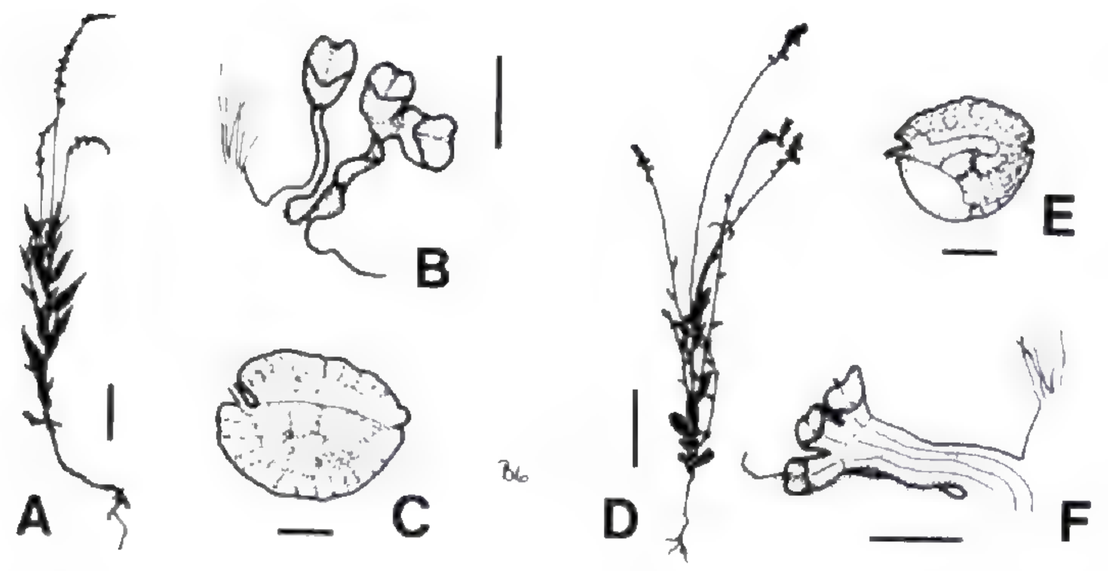


FIGURE 8. *Monnina wrightii* (A–C) and *M. amarella* (D–F). —A, D. Habit. —B, F. Detail of petal-stamen sheath showing a fascicle of stamens with connate filaments. —C, E. Fruits. A, C, *Cabrera et al. 17038* (GH). B, *Arsène 554* (LY). D–F, *Stein et al. 2532A* (MO). Scales: A, D = 5 cm. B, F = 1 mm. C, E = 2 mm.

mán: Catamarca, Mar.–Apr. 1872, *Lorentz 105* (lectotype, selected here, GOET).

*Monnina macrostachya* var. *stenophylla* Kuntze, Revis. Gen. Pl. 3(2): 10. 1898. TYPE: Bolivia. Larecaja (La Seja?), 1892, *Kuntze s.n.* (lectotype, selected here NY).

*Monnina eriocarpa* Chodat, Meded. Rijks-Herb. 27: 29. 1915. TYPE: Bolivia. Santa Cruz: Prov. Florida, Achirastal, 1,300 m, Mar. 1911, *Herzog 1726* (lectotype, selected here, G; isolectotypes, L, S, W).

Nomenclatural note: *Monnina brachystachya* was based on two incongruent elements, viz *Lorentz 105* and *Lorentz 414*. The original description seems to be based on the flowers of #414 and the fruits of #105. *Lorentz 414*, however, belongs to a species different from *M. wrightii*, probably *M. dictyocarpa* Griseb. *Monnina brachystachya* is here typified on *Lorentz 105*, because this collection is the most complete, showing both fruits and flowers (cleistogamous) as well as the habit of the plant. The name *M. brachystachya* has traditionally been applied to the species represented by #105. It was probably the confused original description of *M. brachystachya* that caused Chodat to describe *M. eriocarpa*.

Annual herb, 14–86 cm tall. Stem erect, 1–5 mm diam., terete, usually branched distally, white-pubescent, the hairs curved. Leaves exstipulate; petiole 1–3 mm long, pubescent; laminae on the main axis changing from narrowly ovate at base to very narrowly lanceolate or linear near inflorescence, 1.4–8.5 × 0.2–4.2 cm, chartaceous, acute to acuminate at apex, cuneate at base, the margin and midrib pubescent, otherwise glabrous, the young leaves pubescent throughout. Inflorescence many-flowered, narrowly to very narrowly triangular in outline, 3.5–54 cm long, sometimes very densely pubescent; pedicel 0.5 mm in open flower; bracts very narrowly lanceolate, acuminate to caudate, 1.5–2 mm long, ciliate, undulate, yellowish green mixed with blue. Flowers of the main inflorescence chasmogamous, those of the branches usually cleistogamous (measurements for these given in parentheses); outer sepals unequal, the upper sepal ovate to narrowly ovate, 1–1.5 × 0.5–1 mm (1–1.5 × 0.4–0.6 mm), boat-shaped, the lower ones lanceolate, 1–1.5 × 0.3–0.5 mm (1–1.5 × 0.2–0.5 mm), all acute at apex, ciliate, yellowish mixed with blue; wings obovate to narrowly obovate, 1.5–3 × 1–2 mm (1.5–2.5 × 0.8–1.5 mm), cuneate to attenuate at base, glabrous, blue; keel 1.5–3 × 0.7–1.5 mm (1.5–2 × 0.4–1.2 mm), emarginate at apex, truncate at base, glabrous, possibly yellow throughout; petal-stamen sheath 1–3/1.5–4.5 mm (0.3–1.5/2.5–3 mm) wide, 1–2/1–2.5 mm (1–1.5/1.2–2 mm) tall, a tuft of hairs present at the upper margin between the two filament fascicles, the petals hirsute adaxially, the lobes blue, otherwise greenish as the filament sheath; stamens 6, or two of them ± reduced or totally absent, the upper part of the filaments of the outer two stamens of each fascicle fused throughout, the third stamen, when present, single, glabrous, 0.7–1.2 mm (0.5–1 mm) long including the anther, the anther to filament ratio 0.3–1 (0.5–1); style 0.8–2 mm (0.5–1.2 mm) long, glabrous, bent 45–90° ⅓ to ⅔ from the base, with or without a cavity at the middle; anterior stylar lobe absent or a very short, blunt tooth, the posterior lobe with a sessile, crested stigma (Fig. 10H). Fruit 1-locular, crescent-shaped in outline, 2–5 × 3–6 mm when mature, pubescent, some fruits rarely uni- or bilaterally glabrous, green, narrowly winged (ca. 1 mm), the margin occasionally erose.

*Distribution.* Southern Peru to central Argentina; Uruguay; Mexico and the southwestern United States. Gravelly slopes in the mountains, 1,000–3,000 m (Fig. 6C). In the north it flowers in September–October, in the south between November and April.

*Monnina wrightii* shows an extreme disjunction in its distribution. The type, in appearance, belongs to the homogeneous Mexican–North American population, while the main population of the species, in which variation among individuals is extensive, is found in Bolivia and Argentina. Since the rest of subgenus *Pterocarya* occurs south of the equator, and the largest variation within the species is found there as well, I presume that *M. wrightii* has been introduced to Mexico and the southwestern United States from the Bolivian–Argentinian population. Grondona (1945) was aware of the wide distribution of this species, considered by him to be *M. brachystachya*, and wrote: "Se extiende desde México por la Región Cordillerana

hasta La Rioja, en el noroeste de la Argentina." He did not realize that an earlier, valid name, *Monnina wrightii*, had been published based on a type from New Mexico.

The species seems rather uncommon in Peru and Uruguay; only a single collection is known from each of these countries.

*Specimen examined.* PERU. CUZCO: Prov. Urubamba, Ollantaytambo, 2,850 m, 26 Apr. 1925, *Pennell 13683* (PH).

*Additional material studied (representative collections).* ARGENTINA. CATAMARCA: *Rodriguez 3344* (GH). JUJUY: *Cabrera et al. 17038* (GH). SALTA: *Meyer 3779* (GH). TUCUMAN: *Schreiter 3317* (GH); *Bailetti 150* (GH). BOLIVIA. COCHABAMBA: *Eyerdam 24954* (UC). LA PAZ: *Mandon 836* (GH). PANDO: *Buchtien 259* (GH). TARIJA: *Fiebrig 2054* (LY). MEXICO. CHIHUAHUA: *Pringle 302* (B). MORELIA: *Arsène s.n.* (LY). URUGUAY. SACUAREMBO: *Osten 6537* (GH).

This species possesses two kinds of flowers, a fact already noted by Grondona (1945). Normal chasmogamous flowers occur on the main inflorescence axis, while small and very reduced cleistogamous flowers occur on the branches. In the cleistogamous flowers the petal-stamen sheath is usually reduced to the filament sheath carrying two fascicles each with two anthers, which in turn are adherent to the stigma. The reduction is not always complete, however. The style is usually C-shaped and very short.

The lectotype of *M. brachystachya* (*Lorentz 105*) lacks the main inflorescence axis and consequently has only cleistogamous flowers. Grondona's illustration is slightly misleading because chasmogamous and cleistogamous flowers are shown on different individuals.

The field notes on colors of the flower are rather sparse. I have not seen this species alive, so the description of the colors is given with reservation.

**10. Monnina pterocarpa** Ruíz & Pavón, Syst. Veg. Fl. Peruv. Chil. 1: 174. 1798. TYPE: Peru. Lima: Provinces Lima and Chancay, *Ruíz & Pavón s.n.* (lectotype, selected here, MA, photo of type seen). Figure 9A–H.

*Monnina angustifolia* DC., Prodr. 1: 340. 1824. TYPE: Peru. *Lagasca 54* (holotype, G-DC, photo US).

*Monnina chanduyensis* Chodat, Bull. Herb. Boissier 2: 167. 1894. TYPE: Ecuador. Guayas, Chanduy, on the coast of the Pacific Ocean, 1865, *Spruce 6398* (holotype, G; isotypes, E, P, W).

*Monnina pterocarpa* var. *exauriculata* Chodat, Bull. Soc. Bot. Genève sér. 2, 25: 202. 1934. TYPE: Peru. Tumbes: Prov. Tumbes, Cancas, 100 m, 11 Mar. 1927, *Weberbauer 7757* (lectotype, selected here F; isolectotype, US).

*Monnina piurensis* Ferreyra, Phytologia 69: 359. 1990.

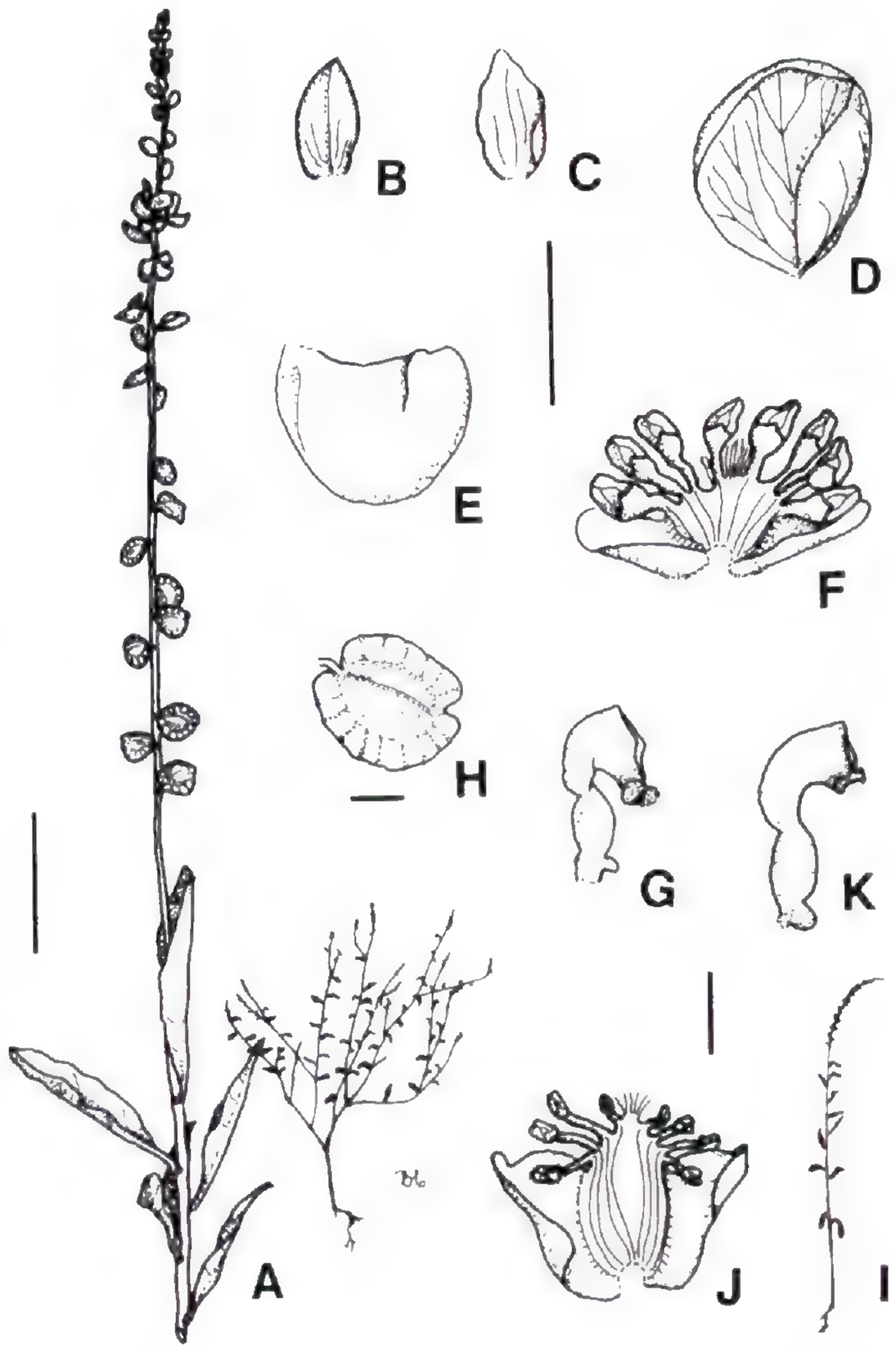


FIGURE 9. *Monnina pterocarpa* (A–H) and *M. herbacea* (I–K). —A. Habit and detail of flowering branch. — B. Upper outer sepal. — C. Lower outer sepal. —D. Wing. —E. Keel. —F. Petal-stamen sheath. —G. Gynoecium. —H. Fruit. —I. Habit. —J. Petal-stamen sheath. —K. Gynoecium. A, H, *Molau & Eriksen 3466* (GB). B–G, *Grant 7393* (GH). I, *Molau & Eriksen 3334* (GB). J, K, *Lagasca 53* (lectotype, G). Scales: A = 2 cm. B–F = 2 mm. H = 2 mm. J, K = 1 mm.

TYPE: Peru. Piura: Prov. Piura, near Piura, *Ferreyra 5882* (holotype, USM; isotype, US).

Annual (or perennial?) herb, ca. 0.5–2.5 m tall. Stem erect, ca. 3–10 mm diam., terete, simple below, loosely branched above, the stem and older branches often glabrous, glaucous, the younger branches sparsely white-pubescent, the hairs curved. Leaves stipulate; petiole 1–3 mm long, pubescent; laminae on the main axis lanceolate to narrowly lanceolate in some plants, narrowly ovate to lanceolate in others, 2–6.5 × 0.2–3.2 cm, chartaceous, acute at apex, cuneate at base, ± pubescent throughout, the branches always with gradually shorter and more narrow laminae toward the inflorescence. Inflorescence many-flowered, very narrowly triangular in outline, ca. 15–40 cm long; pedicel 1 mm; bracts lanceolate, acuminate, 1–3 mm long, ± densely white-hirsute. Flowers all chasmogamous; outer sepals equal in size or the upper

sepal slightly larger, narrowly ovate to lanceolate, 1.2–2.2 mm long, glabrous or rarely sparsely pilose abaxially; wings obovate to broadly obovate, 2–3.5 × 1.5–3 mm, cuneate to truncate at base, glabrous, pink to violet; keel 2.5–4 × 2–2.5 mm, truncate at base, glabrous, emarginate with two lateral lobes at apex, yellow, at least the tip and two lateral spots; petal-stamen sheath 1–2.5/3–7 mm wide, 0.7–3/1–3.5 mm tall, the petals pubescent at the basal margin, the staminal sheath pilose along the midline abaxially (a tuft of these hairs is seen between the filament bundles), the fold marking the line between the petal and filament sheath fringed by long hairs, the petal lobes pink to violet, otherwise greenish as the filament sheath; stamens 8, the upper part of the filaments free, glabrous, 1–1.5 mm long including the anther, the anther to filament ratio 1.0; style 1.5–3.5 mm long, glabrous, ± sigmoid; anterior stylar lobe absent or a very short blunt tooth, the stigma a bilobed disc, sessile or at the tip of a short posterior lobe (Fig. 10I). Fruit 1-locular, compressed, orbicular to rotund, 5–7 × 4–7 mm when mature, glabrous or pubescent, sometimes varying on the same individual, green, occasionally purple-spotted, broad-winged, the wing purple.

*Distribution.* Ecuador, Peru, and Chile. In sand and gravel in dry areas along the coast, or on steep, rocky slopes in the coastal mountains, 0–2,200 m (Fig. 6B).

*Specimens examined.* ECUADOR. GUAYAS: near La Libertad, 23 Feb. 1972, *Beck Breuninger 156* (GB); 11 km N of Sta. Elena, 1 Sep. 1983, *Johnson 2733* (MO, US), 1 July 1984, *Johnson 3300-84* (MO); La Puntilla, near Salinas, 5 Apr. 1941, *Svenson 11221* (US); Punta Centinela, 6 Apr. 1941, *Svenson 11390* (GH, NY, UC, US). PERU. ANCASH: Prov. Bolognesi, km 46 on road from Pativilca to Recuay, 580 m, 27 Jan. 1983, *Dillon et al. 3074* (F, MO), 1,400 m, 9 July 1982, *Gentry et al. 37308* (MO); Colcas, 2,200 m, 19 May 1948, *Pennell 15377* (PH); Prov. Huaylas, Huallanca, km 5 on road to Caraz, 1,700 m, 8 Mar. 1973, *Beck 7892* (GB). CAJAMARCA: Prov. Cajamarca, 50 km SW of Cajamarca, between Magdalena and San Juan, 1,840 m, 5 June 1963, *Ugent & Ugent 5394* (WIS); Prov. Contumazá, 46 km from Pacasmayo on road to Cajamarca, ca. 500 m, 1 Apr. 1988, *Molau & Eriksen 3466* (GB); El Portachuelo de San Antonio, 400 m, 14 May 1983, *Sagástegui et al. 9184* (MO); Ascope–Algarrobal, 150 m, 29 Dec. 1983, *Sagástegui & Mostacero 11336* (MO, US); Quebrada de Chuquimango, 770 m, 5 May 1984, *Sánchez Vega 3400* (MO). ICA: Prov. Nazca, 14 km N of Nazca, 600 m, 22 Nov. 1964, *Hutchison & Wright 7116* (F, UC); Puquio Valley, 1,300 m, 10 Mar. 1954, *Rauh & Hirsch P405* (F). LA LIBERTAD: Prov. Trujillo, El Portachuelo, Ascope–San Benito, 600 m, 11 Aug. 1957, *López 1274* (UC); Cerro Chupitur, Salaverry, 500 m, 24 Feb. 1983, *López 9156* (MO); Cerro Cabezón, 700 m, 20 Feb. 1983, *Sagástegui & Mostacero 10453* (MO, US). LIMA: Prov. Huarochiri, Chosica, 900 m, 1 Feb. 1976, *Gentry 16385* (MO), 28 Apr.–2 May 1922, *Macbride & Featherstone 494* (F), 11–13 Mar. 1923, *Macbride & Featherstone 2874* (F, US); near Sta. Eulalia, above Chosica, 1,100–1,400 m, 2 Apr. 1939, *Goodspeed 11308* (F, GH, NA, UC), 1,100–1,200 m, 10 Apr. 1977, *Gentry et al. 19152* (F, MO), ca. 900 m, 5 Oct. 1935, *Mexia 4007* (GH, MO, UC), 22 May 1963, *Ugent & Ugent 5283* (UC, WIS), 30 July 1941, *Grant 7393* (F, GH, UC), 800 m, *Soukup 2049* (F, GH); above the village Sta. Eulalia, 1,500 m, 15 May 1942, *Goodspeed 33143* (GH, MO, UC); Santa Eulalia–San Juan de Iris road, 1,200 m, 24 Apr. 1982, *Smith & León 1346* (MO), 1,300 m, 24 Apr. 1982, *Smith & León 1356* (MO); Prov. Lima, 20 km NE of Trapiche on road to Huaral, Canta Valley, 1,000 m, 5 Aug. 1957, *Hutchison 1024* (F, UC); Canta Valley, 70 km from Lima, 1,100 m, 7 Oct. 1956, *Køie s.n.* (B); Quives, 800–1,000 m, 9 June 1925, *Pennell 14298* (F, GH, PH); Lima, 1838–42, *sine coll.* (GH); sine loc., *Pavón s.n.* (G). PIURA: Prov. Paita, between Amotape and Talara, 100 m, 19 Apr. 1949, *Ferreyra 5938* (F); Paita, 0–20 m, 4 July 1925, *Pennell 14812* (F, GH, LE, PH, US); Prov. Talara, Talara, 1925, *Haught 7* (F), 11 Oct. 1925, *Johnston 3512* (F, GH), 100 m, 1 Feb. 1954, *Rauh & Hirsch P22* (F); Negritos, 23 Dec. 1928, *Haught F91* (F); road Sullana–Talara, 14 Oct. 1983, *Sagástegui 10900* (MO). TUMBES: Prov. Contralmirante Villar, Zorritos, 100 m, 8 May 1957, *Ellenberg 1327* (U). Department unknown: sine loco, *Martinet s.n.* (F).

Because of the size of the plant, the basal parts are usually not present in herbarium specimens. It is therefore difficult to see whether the plant is annual or perennial. It is hard to believe that a 2.5-m-tall plant with a more or less woody base could possibly sprout and mature in one short season in a dry area. On the other hand, I have seen several withering plants devoid of leaves in a natural population, and the root system seems too tiny for a perennial. Collectors disagree on the subject; some noted "annual," others "perennial" on the labels.

It seems as if there is a gradient from very broad-leaved specimens in the north to almost linear-leaved ones in the south of the distribution area. That is, however, an artifact. The Ecuadorean specimens are generally smaller than the Peruvian ones, and the whole plant, instead of a branch, is usually collected. Since the leaves on the main axis are the largest of the plant, the specimens from the north seem extraordinarily broad-leaved.

Bracts vary in length from 1 to 3 mm and tend to be longest in specimens from the north. The transition is gradual, however.

Ferreyra (1990) described the species *M. piurensis* on the basis of larger leaves and longer bracts relative to *M. pterocarpa*. *Monnina piurensis* is, for the reasons mentioned above, included here in *M. pterocarpa*.

The color of the flowers fades after drying and is mostly very poorly described on the labels. According to the notes I have seen, pink flowers with a brownish yellow keel are common. It is, however, my experience that the brownish tinge of the yellow keel is due to post-pollination color change. The plants I saw had more violet flowers, the keel with a yellow tip and two lateral, yellow spots. Variation in flower color is also seen in *M. macrostachya*.

In a few specimens, unhatched insects (Hymenoptera–Chalcidoidea, determined by T. Hagström) were found inside the flowers. This group of insects is richly represented in the tropics and, according to Hagström, taxonomically very difficult. As it is known to contain both parasitizing and pollinating species, it is not known whether the presence of the insects is a matter of pure parasitism or part of the pollination syndrome.

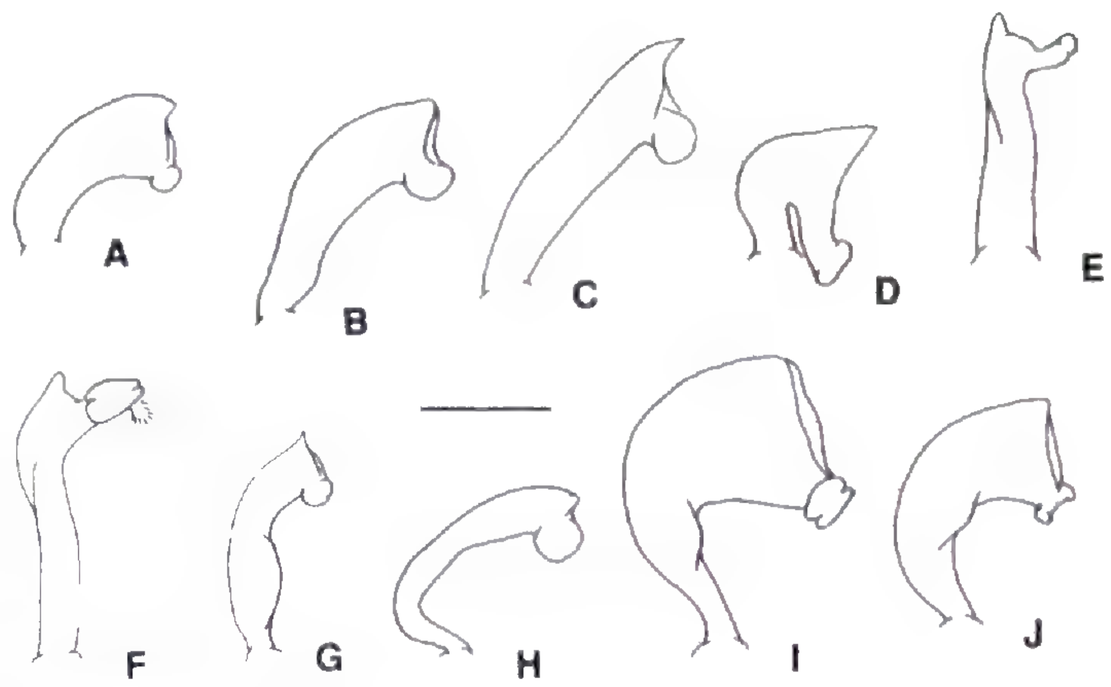


FIGURE 10. Styles and stigmas of *Monnina* subg. *Pterocarya* in northwestern South America. —A. *Monnina fosbergii*. —B. *M. leptostachya*. —C. *M. polygonoides*. —D. *M. ramosa*. —E. *M. macbridei*. —F. *M. macrostachya*. —G. *M. amarella* and *M. filifolia*. —H. *M. wrightii*. —I. *M. pterocarpa*. —J. *M. herbacea*. Scale = 1 mm.

**11. Monnina herbacea** DC., Prodr. 1: 340. 1824. TYPE: Peru. Lima: near Lima, *Lagasca 53* (holotype, G-DC). Figure 9I–K.

*Monnina spruceana* Chodat, Bull. Herb. Boissier 2: 167. 1894. TYPE: Ecuador. Ecuadorean Andes, 1857–1859, *Spruce 5977* (holotype, G; isotypes, E, GH, GOET, LE, NY, S, US, W).

*Monnina graminea* Chodat, Bot. Jahrb. Syst 42: 103. 1909. TYPE: Peru. Cajamarca: Prov. Hualgayoc, San Miguel, 2,200 m, *Weberbauer 3919* (lectotype, selected here, MOL; isolectotype, USM).

Annual herb, ca. 20–100 cm. Stem erect, 1–4 mm diam., terete, slightly furrowed by decurrent leaves, unbranched or branched distally, white-pubescent, the hairs curved. Leaves stipulate; petiole usually 2 mm long, pubescent; laminae lanceolate to narrowly lanceolate, 0.1–2.0 × 1.2–5.2 cm, chartaceous, acute to acuminate at apex, cuneate at base, glabrous except at the margin and the midrib below, the young leaves pubescent throughout. Inflorescence many-flowered, narrowly triangular in outline, ca. 15–50 cm long; pedicel 1 mm long; bracts narrowly lanceolate, 1–2 mm long, acuminate, dark bluish-tinged, ciliate and often sparsely pilose abaxially. Flowers all chasmogamous; outer sepals narrowly ovate to lanceolate, slightly unequal in size, the upper sepal 1.5 × 0.5–0.7 mm, the lower ones 1–1.5 × 0.5 mm, glabrous or rarely sparsely ciliate, dark purplish blue; wings obovate, 2.5–3 × 1.5–2 mm, cuneate to attenuate at base, glabrous, dark purplish blue; keel 2.5–3 × 1.5–2 mm, cuneate at base, glabrous, 3-lobed at apex, the central lobe emarginate, bright yellow, the keel otherwise dark purplish blue; petal-stamen sheath 2–2.5/3–4 mm wide, 2/2–3 mm tall, the petals pubescent at lower margin, the lobes hirsute adaxially, dark purplish blue, otherwise yellowish green as the filament sheath, the fold marking the line between the petal and filament sheath fringed by long hairs, the upper margin of the filament sheath provided with long, curled hairs; stamens 8, the upper part of the filaments free, glabrous, 0.8–1.0 mm long including the anther, the anther to filament ratio 0.3–0.5; style 1.5–2 mm long, glabrous, bent 90° at the middle; anterior stylar lobe absent or a very short blunt tooth, the posterior lobe resembling a hammer-head, i.e., a short stalk with a shorter and narrower stalk perpendicular to it, at the tips of which the stigma is found (Fig. 10J). Fruit 1-locular, ± crescent-shaped in outline, 3–5 × 2–4 mm when mature, glabrous or pubescent, sometimes so on the same inflorescence, wingless, or irregularly or regularly winged, green with purple lines or spots, the wing, when entire, purple-margined.

*Distribution.* Central Ecuador to central Peru. Gravelly slopes in the mountains, ca. 1,200–2,800 m (Fig. 6E).

*Specimens examined.* ECUADOR. CHIMBORAZO: Nariz del Diablo, 2,000 m, 2 June 1939, *Asplund 6848* (US); canyon of Río Chanchán near Huigra, 1,200–1,350 m, 7–14 May 1945, *Camp E-2940* (NY), *Camp E-2954* (F, GH, NY, US), *Camp E-2956* (MO, NY, U, UC), *Camp E-2996* (NY); Simbambe, 2,500 m, 1 June 1947, *Fosberg 27655* (US), 2,000 m, 28 May 1942, *Haught 3323* (BR mixed coll., F, GH, US); Huigra, 1,200 m, July 1923, *Hitchcock 20612* (GH, NY, US); vicinity of Huigra, Hda. Licay, 19 Aug. 1918, *Rose & Rose 22213* (GH, NY, US), 7 Sep. 1918, *Rose & Rose 23853* (GH, NY, US). LOJA: Road Amaluza–Machay–Jimbura, near Machay, ca. 2,000 m, 29 Feb. 1988, *Freire Fierro 1084* (AAU, GB). PERU. ANCASH: Prov. Huaylas, trail to cave across Río Santo from Mancos, 9 Apr. 1970, *Earle Smith*

*& Blas 4902* (US mixed coll.). CAJAMARCA: Prov. Cajabamba, Chicdén below Sunchubamba, 2,800 m, 10 June 1957, *Ellenberg 1920* (U); Prov. Cajamarca, between Magdalena and San Juan, 1,600–1,700 m, 10 Apr. 1950, *Ferreyra 7076* (F); on the road to Chilete, 1 km below San Pablo, 2,550 m, 14 May 1964, *Hutchison & Wright 5069* (F, MICH, MO, UC, US), *5070* (F); La Peña Negra, 1,730 m, 21 May 1975, *Sagástegui et al. 7923* (MO); Prov. Celendín, above Balsas, 30 km E of Celendín on road to Chachapoyas, 2,300 m, 23 Mar. 1988, *Molau & Eriksen 3383* (GB); Prov. Contumazá, road to Guayabo, 1 km SE of Magdalena, 1,300–1,500 m, 18 Mar. 1988, *Molau, Eriksen et al. 3334* (GB); 3–4 km S of Contumazá along road to Cascas, 2,850–2,900 m, 4 Apr. 1985, *Molau et al. 1798* (GB); between Chilete and San Juan, 16 May 1952, *Ochoa 1500* (F, GH); La Montaña, 2,500 m, 18 May 1979, *Sagástegui et al. 9307* (F, MO); Yetón (San Benito–Guzmango), 2,200 m, 3 Apr. 1981, *Sagástegui et al. 9720* (MO); around Contumazá, 2,600 m, 25 May 1981, *Sagástegui et al. 9851* (MO); San Martín, 2,700 m, 31 May 1988, *Sagástegui et al. 14026* (GB). HUANUCO: Prov. Huanuco, 10 km N of Huanuco on road to Tingo Maria, 1,900 m, 13 Apr. 1977, *Gentry et al. 19255* (MO). LAMBAYEQUE: Prov. Lambayeque, between Olmos and Pacora, 1,500 m, 10 June 1978, *Gentry et al. 22621* (F, MO, US). LIMA: Prov. Canta, along Río Chillón, near Viscas, 1,800–2,000 m, 10–15 June 1925, *Pennell 14467* (F, GH, PH, US); Province unknown, *Dombey 625* (F, P). PASCO: Prov. Paucartambo, between Corhuamayo and Paucartambo, *Ochoa 1035* (F, GH).

*Monnina herbacea* is, together with *M. pterocarpa*, unique among the species of subgenus *Pterocarya* in northwestern South America because of having stipulate leaves. Stipulate leaves are more common among the species in the eastern distribution area.

The main difference between the two species mentioned is the construction of the anterior stylar lobe and the position of the stigma. In *M. herbacea* the anterior stylar lobe resembles a hammer-head with rounded stigmas at the tips, while the stigma of *M. pterocarpa* is a sessile or short-stalked, bilobed disc (Fig. 10I, J). Furthermore, *M. herbacea* is in all parts smaller, the flowers are of more delicate texture with differences in proportion and shape of many details, and the stipules tend to be longer. They are also separated altitudinally, with *P. pterocarpa* primarily occurring from the coast up to 1,500 m (rarely higher) and *M. herbacea* above 1,500 m (occasionally lower). Overlap exists, and the two species are even sympatric in some areas.

The name *M. herbacea* has, since the species was described by de Candolle in 1824, been assigned to almost every small, annual species in the subgenus except the taxon of the type. Chodat (1896) placed it among the species lacking stipules, but my studies of the type at G-DC revealed that stipules are present. In 1894, Chodat described *M. spruceana* from Ecuador, and later (1909) *M. graminea* on material from northern Peru, both stipulate. Together with the type of *M. herbacea* from the Lima area they constitute a single, uniform taxon. Ferreyra (1946, 1953), based on Chodat's erroneous note on lack of stipules, and the wingless fruits mentioned in the diagnosis, applied the name mostly to specimens of *M. leptostachya* and *M. polygonoides*.

Vernacular name: "palomilla."

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# THE MISCONSTRUED AND RARE SPECIES OF *COMMELINA* (COMMELINACEAE) IN THE EASTERN UNITED STATES[1]

*Robert B. Faden*[2]

## Abstract

Five species of *Commelina* (Commelinaceae), all introduced in the eastern United States, are reviewed and discussed. The widespread but overlooked *C. caroliniana* is contrasted with the more common *C. diffusa*, and the species are found to be distinguished best by their seeds. *Commelina gigas* is determined to be a polyploid of *C. diffusa*, and the new combination *C. diffusa* var. *gigas* is made. Variety *gigas* is considered likely to have been separately introduced. *Commelina benghalensis* probably became naturalized in Florida early this century. Of the two recently discovered species, *C. forskaolii* is known from a single Florida population that may have been eradicated, and *C. nigritana* var. *gambiae* is becoming well established along roadsides in Florida. Maps of the eastern North American distributions of *C. caroliniana*, *C. diffusa* var. *gigas*, *C. benghalensis*, *C. forskaolii*, and *C. nigritana* var. *gambiae* are provided. Chromosome counts are reported for *C. caroliniana* ($2n$ = ca. 86), *C. diffusa* var. *diffusa* ($2n$ = 30), *C. diffusa* var. *gigas* ($2n$ = 90), *C. benghalensis* ($2n$ = 22), *C. forskaolii* ($2n$ = 30), and *C. nigritana* var. *gambiae* ($2n$ = 56), all first reports from the United States.

The purpose of this paper is to supply background information about five misunderstood or rare species of *Commelina* in the eastern United States. All of them will be fully described in my treatment for the *Flora of North America*, so detailed descriptions have not been included. Instead, data are provided and discussed that cannot be contained in the flora because of format and length restrictions. All five species treated here were introduced in the eastern United States. Among other naturalized species, only *C. communis* L. is not considered, because it is widespread and well known. *Commelina diffusa* Burm. f., the second most common and widespread introduction, is discussed only in the context of its separation from the often overlooked *C. caroliniana* Walter and its relationship with the enigmatic Florida plant *C. gigas* Small. Among the five taxa dealt with in detail herein, three were either misinterpreted (*C. caroliniana*), or ignored (*C. gigas*), or overlooked (*C. benghalensis* L.) in the most recent monograph of the U.S. species (Brashier, 1966). The other two, *C. forskaolii* M. Vahl and *C. nigritana* Benth., had not yet been collected by 1966.

## Distinctions Between *Commelina caroliniana* and *C. diffusa*

*Commelina caroliniana* was recently shown to be a distinct species in the eastern United States and an old introduction from India (Faden, 1989). It is a widespread weedy plant (Fig. 1), yet it remains poorly understood. Undoubtedly this is because of its close resemblance to the even more widespread *C. diffusa*. Both species are usually annual, diffusely spreading plants that root at the nodes. Both have spathes that are solitary (not clustered), simply folded (i.e., margins not fused), and usually acuminate at the apex; small flowers with three blue petals (as contrasted with *C. communis* L., which has a white lower petal); and typically five-seeded capsules with the dorsal locule one-seeded and indehiscent and ventral locules two-

[1] I thank R. P. Wunderlin, J. Beckner, and J. Popenoe for assistance with the fieldwork in Florida in 1983; R. D. Thomas and R. P. Wunderlin for supplying living material of *C. caroliniana* and *C. diffusa* var. *gigas*, respectively; A. R. Tangerini for the maps and line drawings; R. Oliver for technical assistance with the chromosome counts; the curators of the following herbaria for assistance during visits to their institutions or for supplying loans of specimens: CHARL, CLEMS, DUKE, F, FLAS, FSU, FTG, GH, LSU, LTU, MO, NCU, NLU, NY, PH, TENN, UARK, USF, and VPI; and A. J. Faden for heroically caring for the living plants for many years.

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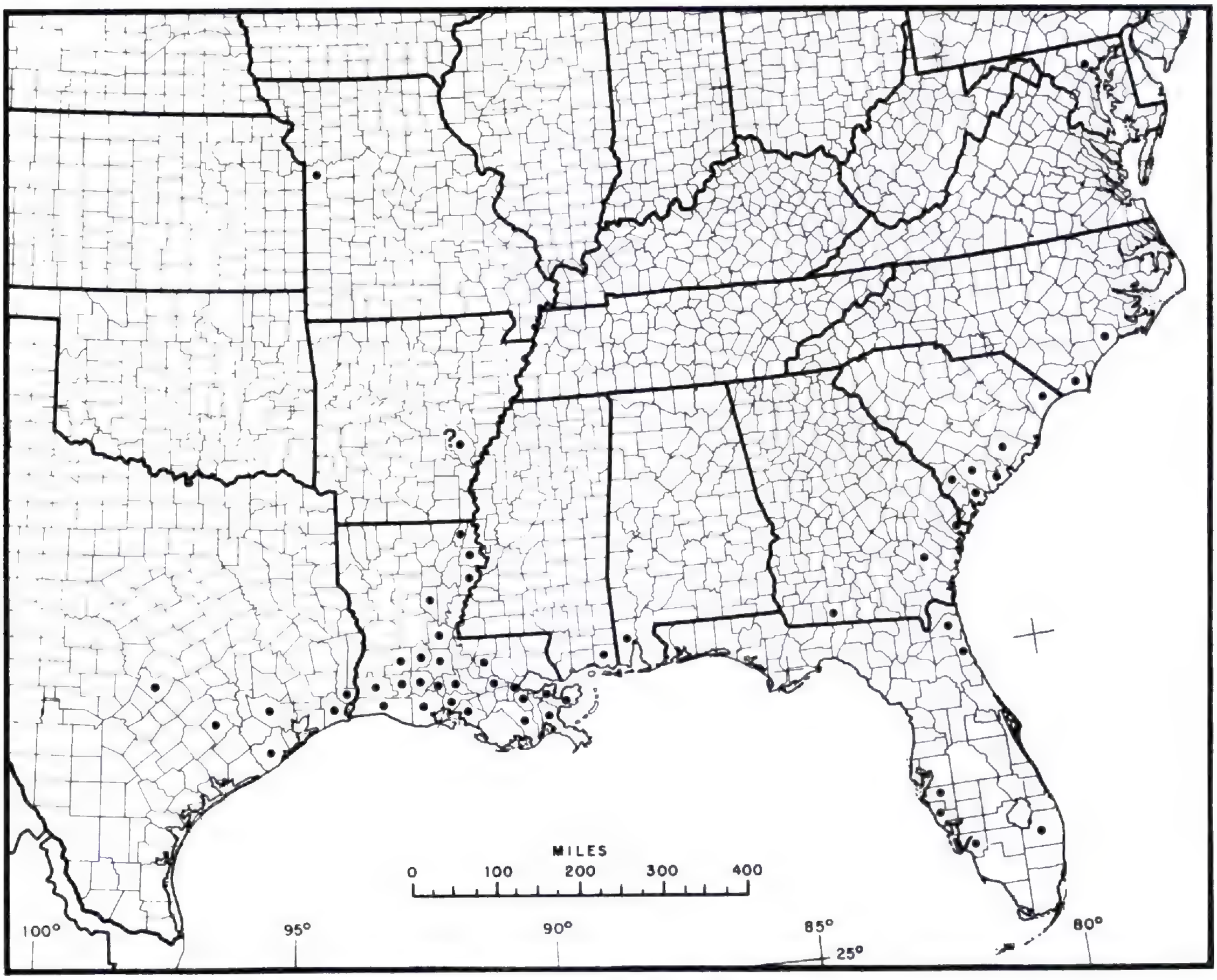


FIGURE 1. Distribution of *Commelina caroliniana* in the United States.

seeded and dehiscent. Because authors have been concerned mainly with separating *C. diffusa* from *C. communis*, it is hardly surprising that cryptic *C. caroliniana* has been overlooked.

It may be noted that reviewer Austin questioned whether *C. diffusa* truly is annual in southern Florida. In my experience, this species is usually perennial in the tropics, so potentially it could persist year-round in the deep South. To determine whether it does indeed survive mild winters in this region, one would need to make long-term observations of populations. Further north, both *C. diffusa* and *C. caroliniana* clearly are annual because they lack subterranean, perenniating organs.

The only modern floras in which *C. caroliniana* has been correctly circumscribed are Gleason (1952, 1963), Gleason & Cronquist (1991), and Steyermark (1963). Radford (1968) considered it a doubtful species. In all of these works, except Gleason & Cronquist (1991), *C. caroliniana* and *C. diffusa* were distinguished by supposed differences in habit and spathe length, characters that do not work. Brashier (1966) considered *C. caroliniana* to be a synonym of *C. diffusa*.

The distinguishing features that may be used to separate *C. caroliniana* from *C. diffusa* are summarized in Table 1. The most absolute difference between them is the testa (Fig. 2). In addition to being nearly smooth (vs. reticulate), the seeds of *C. caroliniana* are also larger and darker brown than those of *C. diffusa*.

The spathes of both species are distinctive, and thus flowering specimens almost always can be identified. The spathes of *C. caroliniana* characteristically lack an exserted upper cincinnus (helicoid cyme) and have a lower edge (i.e., the spathe midrib) that is nearly straight to only slightly curved (Fig. 3A–C). The spathes are not strongly falcate. In contrast, the spathes of *C. diffusa* typically have an exserted upper cincinnus bearing one to several flowers. The lower edge of the spathe is moderately curved, making the spathes distinctly falcate (Fig. 3D–F). Specimens of *C. diffusa* with very small spathes that lack an exserted upper cincinnus normally also bear larger, more typical spathes.

The spathe margin is commonly ciliate basally in *C. caroliniana* (at least a few long hairs present) and usually ciliolate to glabrous (rarely ciliate) in

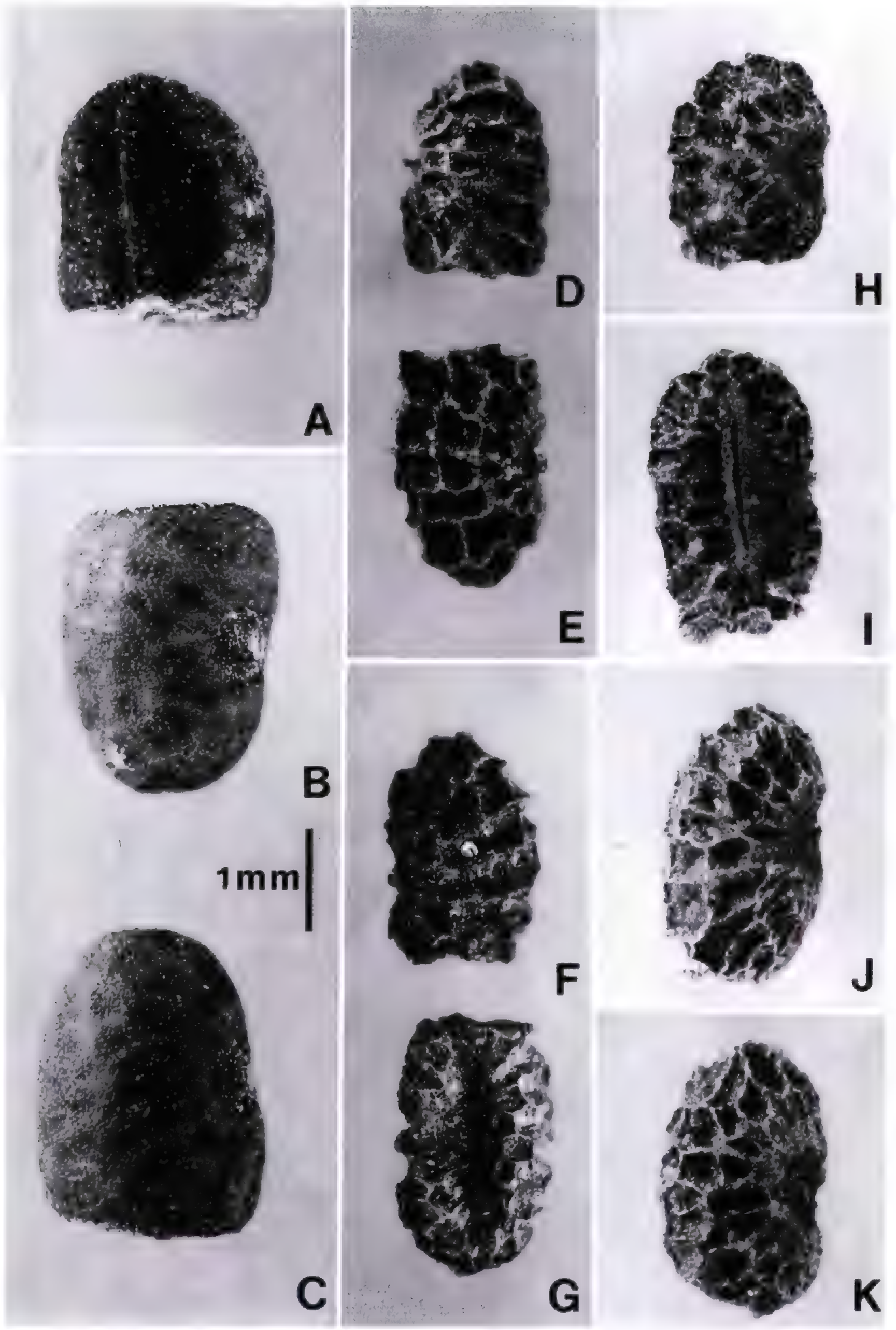


FIGURE 2. Seeds of *Commelina* species in the United States.—A–C. *Commelina caroliniana* (*Thomas et al. 86831*, US).—D–G. *Commelina diffusa* var. *diffusa* (*Faden & Faden 76/1*, US).—H–K. *Commelina diffusa* var. *gigas* (*Faden et al. 83/35*, US). All to the same scale.

*C. diffusa*. The hairs on the peduncles of the spathes are longer in *C. caroliniana* (to 0.5 mm long) than in *C. diffusa* (to ca. 0.1 mm).

The floral differences between the two species, listed in Table 1, need further verification. Although the floral morphology of *C. diffusa* has been recorded from numerous populations in the Paleotropics, it has been observed in only a few, scattered populations in the United States. Similarly, living material from only three populations of *C. caroliniana* (all from Louisiana, supplied by R. Dale Thomas) has been studied. Populations of *C. diffusa* typically have some or all flowers with the medial staminode vestigial or lacking. The antherodes (staminode anthers) in this species never have a central maroon spot. The medial stamen anther normally has a violet to maroon connective (but see *C. gigas* below).

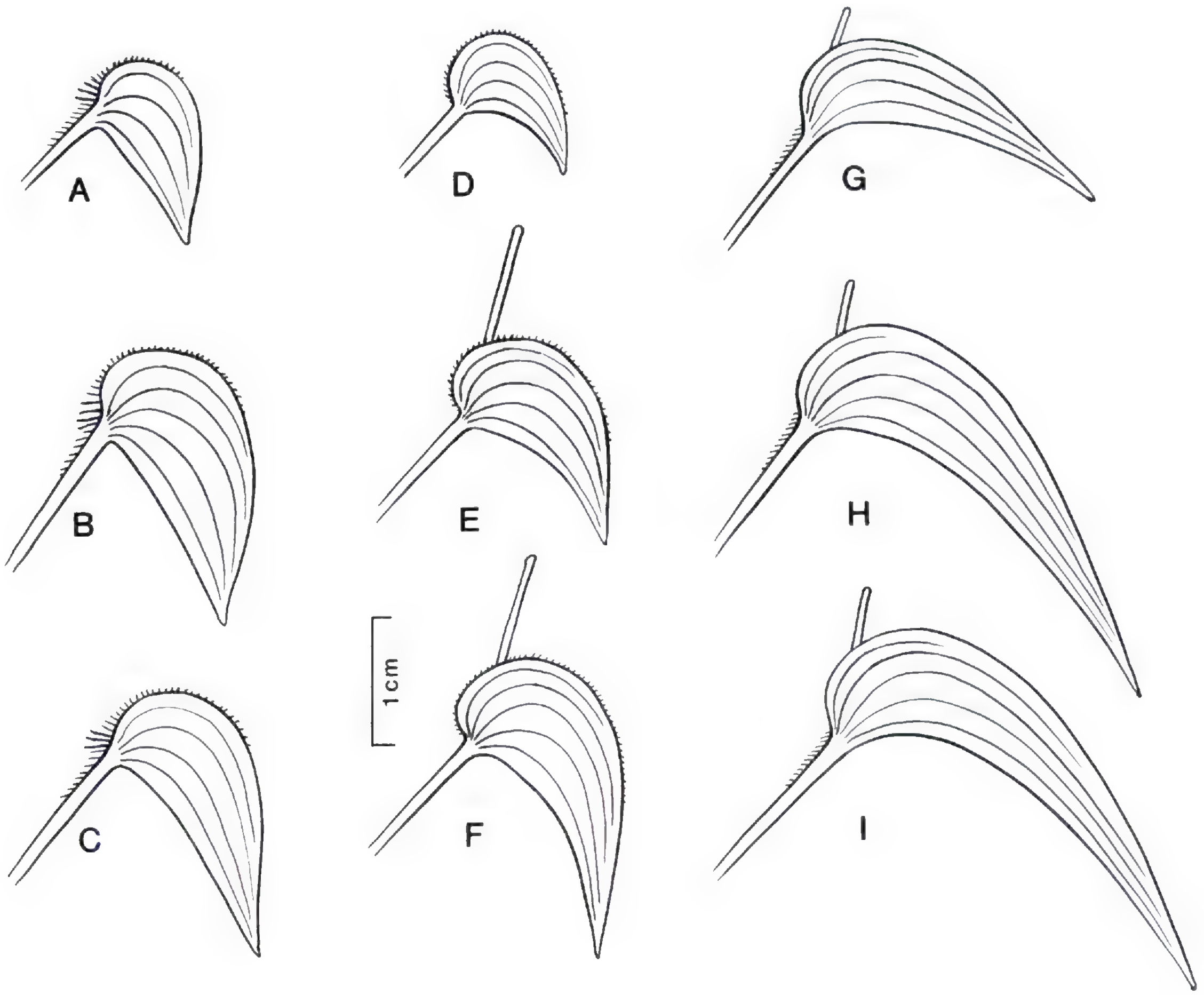


FIGURE 3. Spathes of *Commelina* species in the United States.—A–C. *Commelina caroliniana* (A, *Garber s.n.*, US; B, *Mellichamp s.n.*, US; C, *Curtiss 5177*, US).—D–F. *Commelina diffusa* var. *diffusa* (D, *Smith 486*, US; E, *Plowman 13267*, US; F, *Anderson 10893*, US).—G–I. *Commelina diffusa* var. *gigas* (*Faden et al. 83/35*, US). All to the same scale.

In *C. caroliniana* the flowers from all three populations observed had three equal staminodes with fully developed, 4–6-lobed antherodes. In two of the populations the antherodes had a central maroon spot; in the third population the antherode lobes were entirely yellow. In *Garber s.n.* (US) from Florida, the yellow antherodes of pressed flowers show a central blue spot. In all three living collections, the medial stamen anther consistently had a white connective. It is probable that at least some floral differences noted between the two species will be confirmed from further observations.

Cytological differences between the two species have also been found. Although *C. diffusa* has been reported to have many different chromosome numbers in various parts of its pantropical and warm temperate range (see Faden & Suda, 1980, for summary), the only count for typical material from the United States is $2n = 30$ (two populations from Florida: *Faden et al. 83/32*, *J. Thomas s.n.*, vouchers at US). An exact count was not obtained for *C. caroliniana*, but $2n =$ ca. 86 was secured for all three Louisiana populations (*R. D. Thomas 86722*, *R. D. Thomas et al. 86830*, *R. D. Thomas et al. 86831*, all US). This agrees in ploidy (but not exact number) with two reports from India of $n = 45$ for this species (as *C. hasskarlii*) (see Rao et al., 1968, for summary). Based on preliminary data, typical *C. diffusa* is diploid in the United States while *C. caroliniana* is hexaploid and probably also aneuploid.

Only one specimen that is probably *C. caroliniana* cannot be identified with certainty. Unfortunately, *Toler 45* (UARK) would represent the sole record from Arkansas (see Fig. 1). The single spathe of this flowering specimen is typical for *C. caroliniana*, but the spathe base is broken, and the marginal hairs cannot be checked. Better material

TABLE 1. Differences between *Commelina diffusa* and *C. caroliniana*.

| *COMMELINA CAROLINIANA* | *COMMELINA DIFFUSA* |
|---|---|
| Spathes not at all to slightly falcate, margins usually ciliate basally | Spathes usually distinctly falcate, margins glabrous or ciliolate (rarely ciliate) |
| Upper cyme usually vestigial (rarely well developed and 1-flowered) | Upper cyme in larger spathes well developed and 1–several-flowered |
| All 3 staminodes with well-developed antherodes, antherodes yellow, usually with a central maroon spot | Middle staminode commonly lacking or without antherode, antherodes entirely yellow |
| Middle anther connective white | Middle anther connective maroon to violet |
| Capsules (5–)6–8 mm long | Capsules 4–6.3 mm long |
| Ventral locule seeds smooth to faintly alveolate, 2.4–4.3(–4.6) mm long | Ventral locule seeds deeply reticulate, 2–2.8(–3.2) mm long |

is needed to confirm this species from the state, which would appear to be a reasonable extension of its confirmed range.

The record from Jackson County, Missouri, is based on two collections (one sterile and thus uncertain) from Sheffield (*Bush 3307*, *3332*, both GH, NY), which the collector (in 1905) noted as introduced. In *Flora of Missouri*, Steyermark (1963) treated this as an introduced species. It has not been re-collected in the state. Curiously, there is a very old specimen (*Nuttall s.n.*, PH) of *C. caroliniana* labeled "Missouri" but without further locality information. The state of Missouri would seem to be a very unlikely location for such an early collection of this species.

The specimen *Tracy 5122* (NY) is annotated as having been used for the illustration of *C. caroliniana* in Gleason (1952, 1963). This is the only previously published illustration of this species based on North American material.

*Commelina caroliniana* shows a limited amount of morphological variation throughout its North American range (in comparison with that shown in India). This suggests a single introduction. If the highly unusual chromosome number $2n = 86$, which would be a unique number in the genus, can be confirmed and is found to be general among American populations of this species, that would provide further evidence for a single introduction.

Plants of *C. caroliniana* occur in many different habitats, such as fields, roadsides, yards, waste places, especially in moist situations, and as a weed in crops, partcularly rice, sugarcane, and corn. Flowering occurs mainly from July to November.

## THE STATUS OF *COMMELINA GIGAS*

*Commelina gigas* was described by Small (1933) from hammocks of the Lake Okeechobee region of Florida. The plant, which has never been reported outside of Florida, has remained shrouded in obscurity since its description, being either ignored entirely (e.g., Brashier, 1966; Shetler & Skog, 1978) or listed without comment (e.g., Faden, 1982; Kartesz & Kartesz, 1980; Wunderlin, 1982). When I began work on the Commelinaceae of the southeastern United States, I recognized that Small's species required a critical reevaluation.

Surveys of endangered species of Florida had called attention to *C. gigas* as possibly endangered (Austin et al., 1980; Ward, 1978). This culminated in a brief paper by Austin (1985) in which *C. gigas* was claimed to be no more than a giant form of the introduced weed *C. diffusa*. While I agree with Austin that *C. gigas* is conspecific with *C. diffusa*, I find it more distinctive than he did. This is particularly true when specimens of *C. caroliniana*, which Austin did not recognize, are removed from consideration, and only those belonging to *C. diffusa* and *C. gigas* are compared.

*Commelina gigas* is a robust, spreading, apparently perennial herb that sometimes scrambles in shrubs. Its spathes are solitary, simply folded, falcate and very long and narrow (Fig. 3G–I). The upper cincinnus is usually exserted and one- to three-flowered. The flowers have three blue petals. The medial staminode may be lacking, or present and represented only by a filament, or with a reduced antherode (relative to the other two), or fully developed and similar to the lateral antherodes. The medial stamen anther connective is white. The ovaries are 5-ovulate, but the capsules typically have only one or two seeds in them. The testa has a strongly raised reticulum (Fig. 2). The descriptions of the floral parts in *C. gigas* are based on a small number of flowers from two collections of the same population (*Faden et al. 83/35* and

TABLE 2. Differences between *Commelina gigas* and typical *C. diffusa*.

| *COMMELINA GIGAS* | *COMMELINA DIFFUSA* (TYPICAL) |
|---|---|
| Plants sometimes scrambling in shrubs | Plants diffusely spreading, not scrambling in shrubs |
| Leaves 6–14 cm long, 1–3.3 cm wide | Leaves 1.5–5(–8) cm long, 0.5–1(–2.2) cm wide |
| Spathes 2.3–4 cm long, 2.5–6× as long as high | Spathes (0.5–)0.8–2.5(–3.7) cm long, 1.6–2.7(–3.3)× as long as high |
| Middle anther connective white | Middle anther connective maroon to violet |
| Capsules typically 1–2-seeded (through abortion) | Capsules 5-seeded (occasionally less, by abortion) |

*Wunderlin & Beckner 9118*), so the account of the stamens and staminodes should be considered provisional.

The morphological differences between *C. gigas* and typical *C. diffusa* are summarized in Table 2. To these may be added ploidy. A plant of *C. gigas* (*Faden et al. 83/35*, voucher US) has been found to be a euploid hexaploid, with $2n = 90$ chromosomes, while Florida plants of *C. diffusa*, as noted above, were found to be diploid ($2n = 30$).

Except for the color of the middle anther connective, all of the differences between *C. gigas* and *C. diffusa* are quantitative, and all can be explained by the difference in ploidy. The hexaploid is more robust and has larger leaves and spathes. The small number of seeds in the capsules of *C. gigas* could be due to reduced pollen fertility. Pollen from two Florida populations of *C. diffusa* was found to average 94% fertile (range 72–100%, N = 8); pollen from one population of *C. gigas* averaged 64% fertile (range 53–78%, N = 8). In cultivated plants of *C. gigas* few capsules are produced, and those show the same low seed numbers as field-collected specimens.

The seeds of *C. gigas* and *C. diffusa* are indistinguishable (Fig. 2), although Small (1933: 264) had erroneously described those of the former as smooth. Typically, seeds of related species of *Commelina* differ in size or testa pattern, or both. This identity of *C. gigas* and *C. diffusa* seeds, and the types of magnitude of the differences between these plants demonstrate that *C. gigas* cannot stand as a species. However, it does have a distinct range and it is recognizable, both in the field and in the herbarium. I think that *C. gigas* is best treated as a variety of *C. diffusa*.

**Commelina diffusa** Burm. f. var. **gigas** (Small) Faden, comb. nov. *Commelina gigas* Small, Manual Southeastern Flora, 264. 1933. TYPE (cited on p. 1503 of the same book): Florida. Palm Beach Co.: E shore of Lake Okeechobee, 9–10 May 1917, *Small 8247* (holotype, NY).

*Commelina diffusa* var. *gigas* is restricted to south-central peninsular Florida (Fig. 4). A map of its distribution was published by Ward (1978), showing it in all counties surrounding Lake Okeechobee and extending southeastward into Broward County. Ward's map shows a number of county records that I was unable to confirm from specimens present in 1983 in the three largest Florida herbaria (FLAS, FSU, USF). *Commelina diffusa* var. *diffusa* is distributed from Virginia to eastern Kansas south to Texas, the Gulf Coast and southern Florida.

*Commelina diffusa* var. *gigas* was first collected in 1913 and has been collected rarely since. Only 13 collections have been seen. Its undercollection may be due in part to its apparently sparse flowering—even the type specimen is sterile—as well as to its preference for wet habitats, such as cypress swamps, riverbanks and lakeshores. John Beckner (pers. comm.) stated that *C. diffusa* var. *gigas* easily could have achieved its present distribution by dispersal along waterways. Flowering specimens have been seen from March to May, August, November, and December.

The origins of *C. diffusa* var. *gigas* have not been determined. Either it arose in situ through polyploidy, or else it was introduced and thus not derived from local *C. diffusa*. I believe that it is more likely to have been introduced, because direct origin of a hexaploid from a diploid is implausible, and neither tetraploids nor plants of intermediate morphology are known. However, I have not been able to find any specimens from elsewhere that exactly match the Florida plants. This is why I have recognized variety *gigas* as distinct. Austin (1985) wrote that he observed plants in Hawaii that were identical to *C. gigas*, but Wagner et al. (1990) recorded the spathes of Hawaiian *C. diffusa*

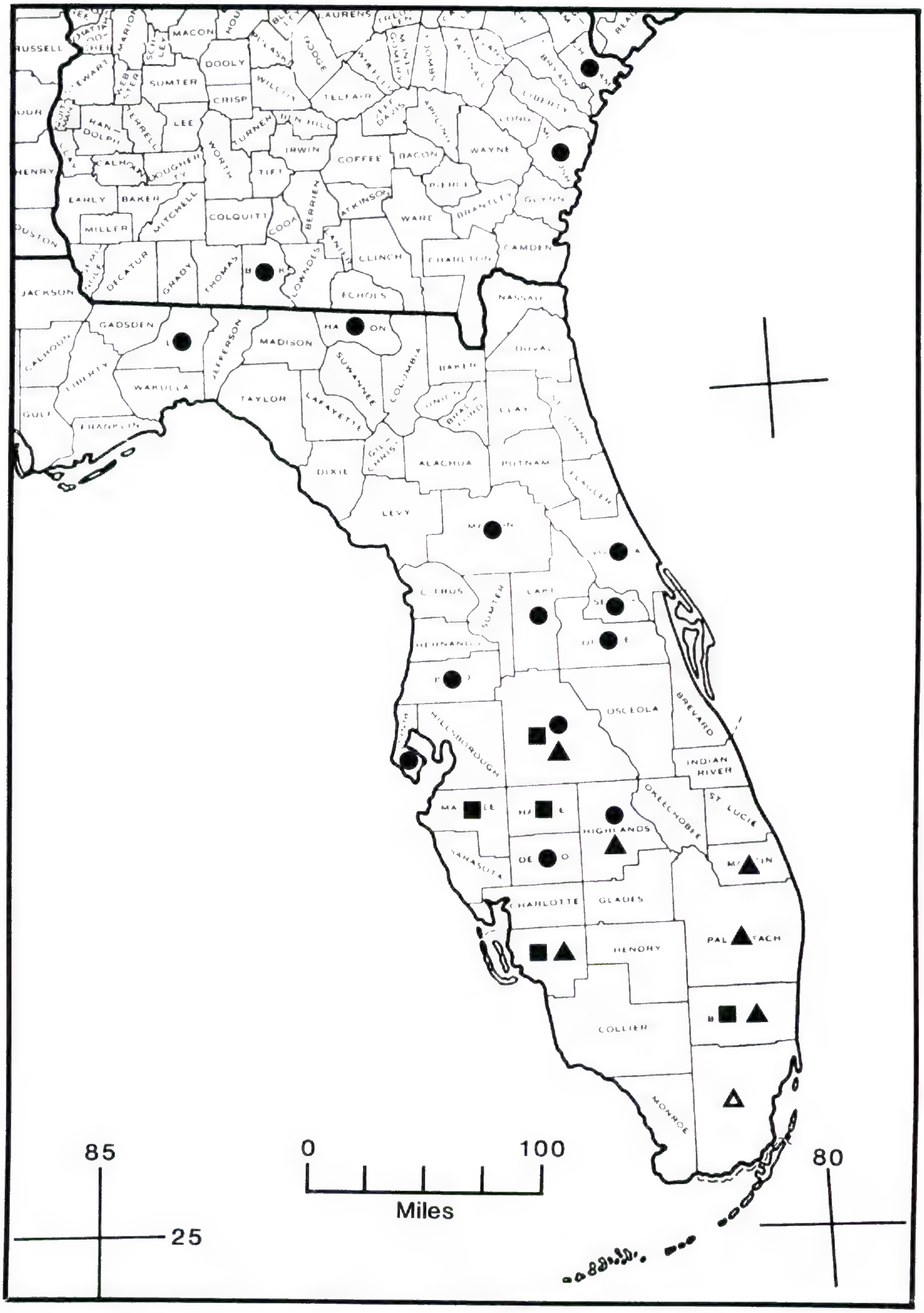


FIGURE 4. Distributions of *Commelina* species in the southeastern United States. *Commelina diffusa* var. *gigas* (solid triangles). *Commelina benghalensis* (circles), *Commelina forskaolii* (open triangle), and *Commelina nigritana* var. *gambiae* (squares).

as 1.5–2 cm long, which is too small for variety *gigas*. The origin of variety *gigas* is likely to have been the Paleotropics, but it cannot be localized further.

## *Commelina benghalensis*: A Well-established Weed in the Southeast

*Commelina benghalensis*, a common paleotropical weed, was reported by Duncan (1967) as a new species for the United States. In 1983 it was designated a "noxious weed," subject to stringent import regulations, by the U.S. Department of Agriculture (Lasseigne, 1983). Despite this fanfare and concern, *C. benghalensis* was first collected in the continental United States in 1928 (*Ruprecht s.n.*, FLAS), and by the mid 1930s it appears already to have become established in Florida. It was first cited from Florida in an unpublished manuscript (McFarlin, 1935), and its floral morphology and floral biology were studied by Uphof (1934), although the plant was misidentified as *C. virginica* L. The earliest record of *C. benghalensis* from the present United States was a pre-statehood, 1909 collection from Hawaii (Wagner et al., 1990).

*Commelina benghalensis* has been collected in at least 12 counties in Florida and three in Georgia (Fig. 4). It grows in fields, yards, other cultivated areas and disturbed sites, and especially in orange groves. This annual species can be recognized by: its funnelform spathes that are often clustered; relatively broad leaves that frequently have red hairs at the summit of the sheath; and cleistogamous flowers that are borne at the base of the plant and are usually subterranean (in addition to normal, aerial, chasmogamous flowers). The plants show a great deal of variation in leaf and spathe size and presence or absence of red hairs on the summit of the sheath and of an exserted upper cincinnus in the spathe. John Beckner (pers. comm.) stated that he thought there were two forms of *C. benghalensis* in Florida, differing in robustness and leaf size.

A study of 25 collections of *C. benghalensis* from Florida and Georgia revealed two extremes of variation: plants with small, obtuse leaves, red hairs on the sheaths, and small spathes lacking an exserted cincinnus; and plants with larger leaves (at least some acute), no red hairs, and larger spathes that frequently contain an exserted cincinnus. Although plants exhibiting these extremes are quite different in aspect, most plants are intermediate. The small-leaved type occurs only at the northern limits of distribution of the species; the larger-leaved type and intermediates are more randomly distributed but are confined to Florida.

It is possible that the extremes of morphological variation represent two separate introductions from the Old World that have since interbred, losing much of their distinctness. However, the morphological plasticity of this weed growing under different conditions has not been investigated, and it is possible that all of the variation observed may be due to environmental factors.

A chromosome count has been obtained for a plant of *Faden et al. 83/33* (US) from De Soto County, Florida, $2n = 22$. This agrees with other published counts for diploids of this species (see Faden & Suda, 1980, for summary).

*Commelina benghalensis* was recently found to be adventive in southern California (Faden & Sanders, in prep.). It is the only introduced species of *Commelina* in the western United States.

## Two Recently Introduced Species: *Commelina forskaolii* and *C. nigritana*

*Commelina forskaolii* is a common species of the drier parts of Africa and southwestern Asia. It is characterized by: small, solitary spathes with fused margins; blue flowers with lyrate, winged, lateral stamen filaments; and capsules in which usually only the dorsal locule seed develops and is shed with the dorsal capsule valve. Many populations also produce subterranean, cleistogamous flowers from the nodes of decumbent shoots.

*Commelina forskaolii* was first collected in the United States from a Dade County (Florida) Sanitary Department landfill in 1980. I first learned of its existence when I was sent a specimen of *Correll & Popenoe 51166*, the first collection, for determination. In November 1983, Popenoe showed us the single known population, from which we obtained specimens and living material. The population was quite extensive. It appeared to have been derived mainly through vegetative reproduction by diffusely spreading stems, although some seeds were present. The plants were very typical of the species, which I know well from Africa. Cleistogamous flowers could not be found. Because this species is considered a significant weed in many parts of its range, I reported it to the U.S. Department of Agriculture. In 1984, it was sprayed with herbicide. Whether it is still extant in the United States is unknown.

A chromosome count was obtained from cultivated material from this population (*Faden et al. 83/26*, US), $2n = 30$, which is usual for this species.

I first became aware of another unusual species of *Commelina* in Florida in 1978 when I was asked what an orange-flowered species in Florida might

be. No specimens were forthcoming, and it was not until several years later that I was reminded of this incident when I received a draft of the Commelinaceae for Wunderlin (1982). The name *Commelina umbellata* Thonn., a synonym of *C. nigritana* Benth., caught my attention. In 1983, accompanied by Wunderlin and John Beckner, I collected three populations of *C. nigritana* from roadsides in Hardee and Polk counties, Florida.

*Commelina nigritana* is a widespread African savanna species and occasional weed. It belongs to a group of annual species with fused spathes and buff- to orange- or apricot-colored flowers. These species also share the unusual basic chromosome number $x = 14$. Two varieties of *C. nigritiana* are recognized by Brenan (1968), variety *nigritana*, with one-seeded capsule locules and pitted seeds, and variety *gambiae* (C. B. Clarke) Brenan, with two-seeded ventral locules and reticulate seeds. All Florida plants belong to variety *gambiae*, the more narrowly distributed form, which occurs in west Africa from Senegal to northern Cameroon.

*Commelina nigritana* var. *gambiae* was first collected in Florida near Bradenton, Manatee County in 1976 (*Wunderlin 5721*, FLAS, TENN, USF). Two years later it was collected in Broward County, on the opposite side of the peninsula. It is now known from at least six counties (Fig. 4) and appears to be spreading rapidly. It has been collected almost exclusively along roadsides, and it is likely to be dispersed by mowing. So far it has not been collected in crops, so its potential to become an important weed is unknown. *Commelina nigritana* var. *gambiae* flowers from September to December.

A Florida plant of *C. nigritana* var. *gambiae* (*Faden et al. 83/27*, US) was found to be tetraploid, with $2n = 56$ chromosomes. The only previous counts for this variety, based on African material, were $2n = 28$, with occasional root tip cells in one population having 56 chromosomes (Morton, 1967).

## Discussion

Among the nine species of *Commelina* in the United States, six are not indigenous: *C. benghalensis*, *C. caroliniana*, *C. communis*, *C. diffusa*, *C. forskaolii*, and *C. nigritana*. Only *C. dianthifolia*, *C. erecta*, and *C. virginica* are native. The recent discoveries of *C. forskaolii* and *C. nigritana* in Florida and of *C. benghalensis* in California should alert botanists, especially in the South, to collect any unusual-looking plants of this genus.

*Commelina*, with 170 species, is the largest genus of Commelinaceae and its species are often difficult to identify. Capsules and seeds are frequently critical, so they should always be looked for when making collections of this genus. Flowers should be pressed separately between absorbent paper or cellophane. Floral features that should be particularly noted are: lateral sepal fusion (when present); paired petal color; lower petal degree of development and color; number of staminodes and color of the antherodes; and color of the anther connectives and pollen.

## Key to the United States Species of *Commelina*

1a. Spathes with margins free to the base.
  2a. Perennials with erect to ascending shoots; roots tuberous; leaves linear to linear-lanceolate ..... 1. *C. dianthifolia*
  2b. Annuals or perennials usually with decumbent to scandent shoots; leaves narrowly lanceolate to ovate-elliptic.
    3a. Spathes generally whitish or pale green towards the peduncle with contrasting, dark green veins; middle petal white or paler than the others; capsules bilocular; seeds rugose foveate-reticulate ..... 2. *C. communis*
    3b. Spathes lacking contrasting veins; middle petal ± concolorous with the others; capsules trilocular; seeds reticulate or smooth to faintly alveolate.
      4a. Spathes not at all to slightly falcate; upper cyme usually vestigial (rarely well developed and 1-flowered); seeds smooth to faintly alveolate ..... 3. *C. caroliniana*
      4b. Spathes usually distinctly falcate; upper cyme in larger spathes usually well developed and 1-several-flowered; seeds reticulate ..... 4. *C. diffusa*
1b. Spathes with margins fused basally.
  5a. Flowers apricot- or peach-colored ..... 5. *C. nigritana*
  5b. Flowers blue (rarely lilac to lavender or white).
    6a. Leaves with auricles at summits of sheaths; roots stout; middle petal white, inconspicuous; locules all 1-seeded ..... 6. *C. erecta*
    6b. Leaves not auriculate; roots thin; middle petal blue to lilac or lavender, conspicuous; some locules usually 2-seeded.
      7a. Perennials with erect to ascending shoots; sheaths with red hairs at the summit; lamina 6–20 cm long; spathes 1.5–3 cm long; underground, cleistogamous flowers lacking ..... 7. *C. virginica*

7b. Annuals or perennials with ascending to decumbent, repent or scrambling shoots; sheaths with or without red hairs at the summit; lamina 2–7(–9) cm long; spathes 0.5–2 cm long; underground, cleistogamous flowers sometimes present.

8a. Lamina ovate to lanceolate–elliptic; sheaths often with red hairs at summit; lateral stamen filaments not winged; capsules usually 5-seeded, the ventral locule seeds developed ..... 8. *C. benghalensis*

8b. Lamina oblong to lanceolate-oblong or oblong-elliptic; sheaths lacking red hairs; lateral stamen filaments winged; capsules usually 1-seeded, only the dorsal locule seed developed ..... 9. *C. forskaolii*

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Appendix. Specimens of *Commelina caroliniana* seen from the United States.

Because of the difficulty in identifying *Commelina caroliniana* with certainty, all American specimens seen of this species are cited below. This is intended to be a means for checking whether particular specimens belong to this species, so only collection numbers and institutional codes are listed. Institutional sheet numbers (when available) are listed where there is no collection number. Specimens from NLU with more than one collection number on the sheet have the additional number(s) in brackets.

Allen 12665 (NLU), Allen s.n. (NLU), Anderson s.n. (MO#1967952), Ahles 36000 (NCU), Ahles & Bell 18355 (NCU), 21053 (NCU), Ashbey 18 (GH, MO), 38 (GH, MO).

Bell 16222 (NCU), 16223 (TENN), Brown 1158 (LSU, NLU), 5946 (LSU), 20180 (LSU), Bush 3307 (GH, NY), 3332 (GH, NY).

Claycomb s.n. (LSU), Cormier 446 (NLU), Correll 36514 (GH), Cory 11038 (GH), 11461 (GH), Curry 310 (LSU), Curtiss 2992 (F, PH), 4144 (MO, NY, US), 5177 (F, FSU, GH, MO, NY, US), 6273 (FLAS, NCU), s.n. (MO#1749041), s.n. (US#223467), Cuthbert s.n. (FLAS#5472).

Duke 228 (NCU), Duncan 30556 (CLEMS), 30601 (NCU), Dutton & Taylor 217 [5334a] (NLU).

Elliott s.n. (CHARL).

Faircloth 6250 (MO), Felix s.n. (FLAS#6661, US#2216458), s.n. (GH).

Garber s.n. (US#33708), Genelle & Fleming 2207 (USF), Gibbes s.n. (NY), Ginn 16 (LSU), Graves 1938 (MO).

Hoffman 12 (FLAS).

Langlois s.n. (GH, PH).

Mellichamp s.n. (US#936363), Mellinger s.n. (GH), Miles 147 (FLAS), Montz 122 (LSU), 3646 (LSU).

Nuttall s.n. (PH).

Pias & Thomas 4482 (LSU), Pias et al. 4417 (LSU).

Ravenel s.n. (NY), Reed 41364 (US).

Shinners 21414 (FSU, GH, USF), Small 241 (LSU).

Tharp 1526 (F), s.n. (US#114521), Thibodeaux 25 (LSU), 132 (LSU), 202 (LSU), 439 (LSU), Thieret 9588 (FSU), 16367a (VDB), Thomas 80000 (NLU), 86722 (US), Thomas & Allen 47784 (NLU), 79277 (NLU), 87174 (NLU), 98115 (MO, NLU), 98208 (NLU), 98330 (NLU), 98444 (NLU), Thomas & Briley 69679 [900] (NLU), Thomas & Laird 50479 [2826] (NLU), Thomas et al. 26933 (NLU), 56572 [2689] (NLU), 61035 [1570] (NLU), 66593 (NLU), 66933 (NLU), 67426 [1528] (NLU), 86830 [777, 6251A] (NLU, US), 86831 [778, 6252] (NLU, US), 91099 [3944] (NLU), 94030 [13236] (NLU), Thompson s.n. (US#1537440), Thompson & Nishida 3045 (US), Toler 45 (UARK), Tracy 5122 (F, MO, NY).

Walter (or Fraser) s.n. (BM-Walter, lectotype of Faden, 1989), Warnock et al. 46372 (NCU), Williams 56 (NLU), no collector or number (PH, Muhlenberg Herbarium No. 92, pro parte).

# *TRADESCANTIA CRASSIFOLIA* (COMMELINACEAE), AN OVERLOOKED SPECIES IN THE SOUTHWESTERN UNITED STATES[1]

*Robert B. Faden*[2]

ABSTRACT

*Tradescantia crassifolia* (Commelinaceae), a widespread species in Mexico, is reported from the United States for the first time, based on two nineteenth-century collections. The specimen from Texas is considered reliably localized; that from New Mexico is deemed questionable.

*Tradescantia crassifolia* Cav., a common species known from Mexico to Guatemala, has not been reported from the United States. In the course of preparing the *Flora of North America* treatment of Commelinaceae, I discovered two old specimens that document this species in the Southwest. I call attention to this record and encourage local botanists to seek this species in order to determine whether it is still extant in the United States. The specimens seen are:

UNITED STATES. TEXAS: Chinati [Chenate] Mountains, *V. Havard*, October 1880 (US sheet #225303) (Fig. 1). NEW MEXICO: Without specific locality, *Edwards*, 1848 (NY).

It is probable that the locality of the Texas specimen is correctly stated. Valéry (often written without the accent mark of the original French) Havard (1846–1927), an Army physician with a background in botany, collected plants in western Texas from 1880 to 1884 (Lanjouw & Stafleu, 1957; McVaugh, 1957). McVaugh, quoting monthly reports filed by Havard (originals in the National Archives), noted that in Havard's report of 30 September 1880 he mentioned a trip made to the Chinati Mountains, and that in a later report he recorded being in these mountains 20–24 December the same year. McVaugh concluded that Havard probably gained most of his knowledge of the Chinati Mountains between September and December 1880, when he was Post Surgeon at Camp Eagle Nest in Presidio. Havard's (1885) "Report on the flora of western and southern Texas" included a brief account of the flora of the Chinati Mountains, demonstrating that he clearly visited the area and could have collected plants there (publication of this in the *Proceedings of the U.S. National Museum* was a direct quid pro quo for Havard's donation of his collections to the Smithsonian Institution, according to correspondence in the Smithsonian Institution archives). There is no evidence that Havard ever collected in Mexico, the only other possible origin of this specimen.

Hunt (in litt., 4 Oct. 1990) stated that a range extension for *T. crassifolia* into Texas and New Mexico would not be unreasonable. In the U.S. National Herbarium there are two Mexican collections of *T. crassifolia* from the Sierra del Carmen, Coahuila, a mountain range very close to Big Bend National Park, Texas, and six collections from the region around Cd. Chihuahua. These Mexican localities are in the same U.S.D.A. Plant Hardiness Zone (Zone 8) (Cathey, 1990) as the Chinati Mountains, which could thereby be expected to support many of the same plant species. Johnston (in litt.) has noted that several Mexican species are known in the United States only from the Chinati Mountains, including *Calliandra coulteri* S. Watson (Fabaceae) and *Argythamnia astroplethes* J. Ingram (Euphorbiaceae).

The New Mexican collection is more problematical. The collector Edwards is Lewis Allison Edwards (fide R. Barneby via M. Nee) (1823–1877), an Army surgeon who was stationed near Monterey, Mexico, during the Mexican War, 1846–1848, and sent plant collections to John Torrey.

[1] I thank reviewer Marshall Johnston and an anonymous reviewer for helpful suggestions.

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FIGURE 1. *Tradescantia crassifolia* Cav. (*Havard s.n.*, US).

He is commemorated by *Cracca edwardsii* A. Gray (fide R. Barneby). Edwards was based in Santa Fe after the Mexican War. On 29 June 1848 he wrote to John Torrey (archives New York Botanical Garden) from Monterrey, Mexico, that "We have just received orders to proceed to California & Santa Fe. . . . We start in about 14 days, passing through Parras, the great vine growing country, Chihuahua, Paso del Norte, &c." Edwards wrote that he hoped to "make amends" during the next 10 months for not having collected many specimens recently. Edwards's actual itinerary was detailed in a 20 October 1848 report (original in National Archives) sent to Thomas Lawson, Surgeon General, U.S. Army, from Santa Fe: "The command left Monterey [sic] on the 25th of July, arriving at the village of Castañuelas on the 31st, a distance of 115 miles. On the 26th of August we reached Chihuahua, remaining at that city until the 1st ultimo. On the 30th of September we encamped at the settlement of Sa Parida, distant from Chihuahua 376 miles. On the 10th inst. we arrived at this place, making in all a distance of about 1050 miles." He was stationed at Santa Fe until September 1850 (Woodward, 1879).

Whether Edwards actually collected plants in New Mexico is uncertain (e.g., he is not included in McKelvey, 1955). Rodgers (1942: 219), stated that Edwards was one of several collectors who collected in the vicinity of Santa Fe, these collections forming the basis of *Plantae fendlerianae* (Gray, 1849), but a perusal of this work revealed that the only Edwards's collections cited are from Mexico. The only other evidence is the label on the specimen of *T. crassifolia* cited above. The problems with that information are: (1) "New Mexico" (as of February 1848) was the newly ceded New Mexico Territory, consisting of most of the present states of New Mexico and Arizona, as well as a small portion of Colorado, and some of western Texas (Wooton, 1906) (the locality is thus rather vague); and (2) the Santa Fe area, where Edwards was based and would have had time to collect plants, appears to be climatically unsuitable for this plant (R. Spellenberg, pers. comm.). The specimen most likely came from further south and was collected en route to Santa Fe. Edwards passed through appropriate habitats for this species (and at the right time of year to find it) around Cd. Chihuahua, where the plant is known to occur. Thus it could have been collected in Mexico and later mislabeled. Hence, the New Mexico record is unproven.

*Tradescantia crassifolia* Cav. (Fig. 1) is easily recognized by a number of features: tuberous roots; distichous, lanceolate to ovate leaves; cobwebby, white pubescence on the vegetative parts (especially the leaf sheaths); sessile cyme-pairs in the axils of the upper 1–5(–7) leaves; pedicels and sepals pilose with eglandular hairs. Although this species is very variable in Mexico, especially in shoot length, leaf shape, and amount of pubescence on the vegetative parts, it is unlikely to be confused with any of the five other species of *Tradescantia* that occur in Trans-Pecos Texas and/or New Mexico. All of these species have some or all of the cyme-pairs stipitate and subtended by foliaceous or spathaceous bracts. In addition, three of them, *T. wrightii* Rose & Bush (Texas and New Mexico), *T. pinetorum* Greene (New Mexico), and *T. occidentalis* (Britton) Smyth (Texas and New Mexico), have linear-lanceolate, glabrous (to scabridulous) leaves, and glabrous to glandular-puberulent sepals. The other two west Texas species, both formerly placed in *Setcreasea* (see Hunt, 1975), *T. brevifolia* (Torrey) Rose and *T. leiandra* Torrey, have terminal or leaf-opposed inflorescences, clawed petals that are gamepetalous basally, and glabrous filaments. In addition, *T. leiandra* has sepals with glandular or eglandular hairs, and *T. brevifolia* has glabrous sepals. *Tradescantia crassifolia* is the only species of section *Mandonia* D. R. Hunt (Hunt, 1980) to occur in the United States.

After this manuscript was completed and reviewed I had the opportunity to reexamine Edwards's collection at the New York Botanical Garden. The sepals and pedicels of the specimen have numerous glandular hairs, a feature that does not agree with *T. crassifolia* or with any other species of section *Mandonia* (Hunt, 1980). Thus, this putative record of *T. crassifolia* from New Mexico is even more doubtful. In view of this new information, I subsequently restudied Havard's specimen and reconfirmed that it is indeed *T. crassifolia*. Although the specimen has only sparsely pubescent leaves (unlike many Mexican collections), it does not match *T. crassifolia* var. *glabrata* C. B. Clarke, which has the lamina glabrous except for a marginal band of dense, white, woolly hairs.

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# EL GENERO *INGA* (LEGUMINOSAE: MIMOSOIDEAE) DEL SUR DE MEXICO Y CENTROAMERICA, ESTUDIO PREVIO PARA LA *FLORA MESOAMERICANA*[1]

Mario Sousa S.[2]

## Resumen

En la preparación del género *Inga* para la *Flora Mesoamericana* se discuten someramente la nomenclatura y taxonomía de cada especie, su variación, asi como la posible influencia del hombre. Fue necesario lectotipificar siete nombres: *Inga alba*, *I. densiflora*, *I. multijuga*, *I. oerstediana*, *I. paterno*, *I. ruiziana*, e *I. vera*. También se cita material representativo de todas las áreas donde habita cada especie, incluyendo las de fuera del área de la Flora. Se describen trece especies nuevas para la ciencia: *Inga bella*, *I. cabrerae*, *I. calcicola*, *I. cuspidata*, *I. chiapensis*, *I. dasycarpa*, *I. davidsei*, *I. dwyeri*, *I. ismaelis*, *I. lacustris*, *I. pseudoinvolucrata*, *I. sinacae*, e *I. tenella*. También se hizo un cambio nomenclatural de *Inga cocleensis* var. *megantha* a *I. cocleensis* subsp. *megantha*.

## Abstract

As a precursor to the treatment of *Inga* for the *Flora Mesoamericana*, this summary of the genus is presented, including the nomenclature, taxonomy, and variation of all the species, as well as the possible influence of humans in altering patterns of distribution and variation. Seven names are lectotypified: *Inga alba*, *I. densiflora*, *I. multijuga*, *I. oerstediana*, *I. paterno*, *I. ruiziana*, and *I. vera*. Representative specimens are cited for all species, including areas outside of Mesoamerica. Thirteen species are described as new: *Inga bella*, *I. cabrerae*, *I. calcicola*, *I. cuspidata*, *I. chiapensis*, *I. dasycarpa*, *I. davidsei*, *I. dwyeri*, *I. ismaelis*, *I. lacustris*, *I. pseudoinvolucrata*, *I. sinacae*, and *I. tenella*. A nomenclatural change was made for *Inga cocleensis* var. *megantha* to *I. cocleensis* subsp. *megantha*.

Para la preparación del tratamiento del género *Inga* (Leguminosae: Mimosoideae) para la *Flora Mesoamericana*, que abarca del Sur de México a Panamá, ha sido necesario realizar este artículo que formaliza taxa y da información complementaria y aclaratoria, que las normas editoriales de la *Flora* no permiten.

El género ha sido tratado en forma integral por Bentham (1845, 1875) y para Mesoamérica por Pittier (1916, 1929) y León (1966), y en floras locales como la de Costa Rica por Zamora (en prensa) y la de Panamá por Schery (1950). En el último tratamiento del área, León (1966) incluye 49 especies, de las cuales nosotros estamos reco-

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nociendo 47, aunque no necesariamente con los mismos nombres; de las 81 especies que aquí se tratan, tal crecimiento en el número de especies, es, fundamentalmente, por el gran acúmulo de nuevas colectas que se han hecho en el área en los últimos 25 años, que han incorporado tanto nuevas especies para la ciencia como varias otras sólo conocidas para Sudamérica. Este nuevo material también ha permitido interpretar mejor la variación de las especies antes sólo conocidas por escaso material, lo que en algunos casos permite sinonimizar binomios de uso local en nuestra área. Sin embargo, lo anterior no significa que ya el tema esté agotado, por el contrario, como hay varios ejemplares que podrían ser nuevos taxa, que no creo conveniente formalizar por lo incompleto del material, y además algunas especies ya descritas sólo son conocidas por el tipo.

Respecto al material representativo se decidió dar mayor información de la que permiten las normas editoriales de la *Flora Mesoamericana*; ésto es debido a que la *Flora* sólo autoriza usar una colecta por cada una de las diez regiones en las cuales está dividida la flora, además de una referencia muy corta de sus límites geográficos extra mesoamericanos. Así se decidió ampliar esta información por considerarse útil tanto en cuanto al concepto de especie como por sus obvias implicaciones de uso y distribución regional. También se cita el material de fuera de la región mesoamericana por considerase de interés dado que no existe actualmente un tratamiento integral equivalente en América del Sur, sólo trabajos regionales como de Bentham (1876) para Brasil, Poncy (1985) para la Guayana Francesa, y de Macbride (1943) para el Perú. Así se cita un ejemplar para cada uno de los estados de México y departamentos, distritos, estados o provincias de cada país centroamericano, así como de los de Sudamérica, haciendo excepción de sólo una colecta para cada una de las Guayanas y países de las Islas del Caríbe. Brasil se dividió en regiones dado la amplitud del país.

El formato de las descripciones sigue al de la *Flora Mesoamericana*; sin embargo, en general los caracteres usados para el género son los empleados por Pittier (1916, 1929), León (1966), y Poncy (1985), aunque no necesariamente su terminología. Así de Poncy adoptamos el concepto de las brácteas homomorfas y heteromorfas que ella maneja en sus descripciones e ilustra en sus láminas; además aquí estamos empleando en forma extensiva el uso de botones florales que parece ser un carácter útil en la taxonomía de *Inga*. Los botones florales sólo son citados ocasionalmente como en *I. acuminata* (León, 1966), pero en general no son descritos, ni menos usados como un carácter diagnóstico. En la descripción de las especies nuevas y de las del tratamiento de la *Flora* este carácter es usado extensivamente, cuando conocido. Su uso es referido como "botones con el cáliz cubriendo" y las opciones son "abierto" o "cerrado"; aquí hay que aclarar que se refiere al estado de desarrollo del botón floral cuando el tamaño del cáliz es aproximadamente un ⅓ menor al del tamaño normal de una flor en antesis, siendo ésto importante ya que, todos los botones realmente incipientes cuentan con un cáliz cerrado. Así se pueden categorizar los botones florales (con algunos ejemplos claros) de la siguiente forma:

1. Cáliz cerrado, botones casi esféricos: *Inga goldmanii*, *I. rubiginosa*.
2. Cáliz cerrado, botones ovoides a obovoides a tubulares: *I. calcicola* (véase Fig. 1D), *I. exalata*.
3. Cáliz cerrado, botones rostrados, los lóbulos unidos en uno: *I. acuminata*, *I. urabensis*, *I. venusta*.
4. Cáliz abierto en un poro, botones tubulares: *I. leonis*, *I. sierrae*.
5. Cáliz abierto, tubular, los lóbulos aplicados a la corola, la que crece con el cáliz: *I. sinacae*, *I. thibaudiana*.
6. Cáliz abierto, tubular, los lóbulos conniventes en sus ápices, el botón obtuso en el ápice, la protocorola más pequeña que el cáliz: *I. fastuosa*, *I. mucuna*.
7. Cáliz abierto, los lóbulos conniventes en sus márgenes, el botón rostrado, la protocorola más pequeña que el cáliz: *I. pavoniana*, *I. tonduzii*, *I. vera*.
8. Cáliz abierto, los lóbulos erectos no conniventes, la protocorola más pequeña que el cáliz: *I. cookii*, *I. ismaelis* (véase Fig. 4A, E), *I. setosa*.

Respecto a los agrupamientos supraespecíficos en *Inga*, el sistema de Bentham (1845, 1875, 1876) modificado por León (1966), necesita más refinamientos, sobre todo en los límites de la sección *Leptinga* con la sección *Bourgonia* (ver discusiones de *Inga acrocephala*, *I. alba*), basados en el tipo de inflorescencia, la cual puede variar de capituliforme a racimos cortos. Por otro lado en la sección *Leptinga* hay varios grupos naturales como él de alrededor de *I. cordistipula* incluyendo: *I. bella*, *I. portobellensis*, *I. pseudoinvolucrata*, e *I. spiralis*. También alrededor de *I. umbellifera* se puede agrupar a otro contingente de especies como:

*I. brevipes*, *I. polita*, *I. sciadion*, e *I. umbratica*. Con *I. saffordiana* quedaría *I. filiformis*, este último grupo muy natural que ha divergido grandemente del resto de la sección. Como sugirió León (1966: 344) todos estos grupos no parecen tener parentesco entre ellos y el tipo de inflorescencia parece más bien un paralelismo.

De los agrupamientos existentes, quizá uno de los más naturales es la serie *Inga*, definida fundamentalmente por la legumbre, pero que a la vez cuenta con las especies más variables y panmixicas del género.

La sinonimia la hemos tratado cuando en forma original estamos agregando información nueva no tratada por Schery (1950), León (1966), o Poncy (1985); así estamos excluyendo la citación de los cambios que Kuntze (Revis. Gen. Pl. 1: 182–189. 1891) hizo a *Feuilleea*. En algunos casos se dan sinónimos ya reportados por otros autores, pero se toma esta libertad para aclarar problemas. También siempre se apunta el basiónimo cuando éste existe, o el homónimo tardío en el cual se basa el nombre en uso.

Las claves fueron elaboradas tratando de agrupar especies afines y por ello su uso se circunscribe a la identificación de especies y en forma limitada a ejemplares, a este respecto hay que apuntar que en una gran proporción los ejemplares sólo cuentan con un estadío, es decir en flor, fruto o, desde luego, estériles. Sin embargo, la elaboración de las claves de sólo flores o frutos nos llevó frecuentemente a por un lado, ubicar a una misma especie en varias entradas, y por otro lado, agrupar varias especies al final de una dicotomía.

Dado el nivel de conocimiento del género *Inga* en Mesoamérica no estamos formalizando categorías infraespecíficas, con una excepción; sin embargo cuando hemos creido que debería hacerse, lo mencionamos en cada caso, dejando la decisión final para quien revise al género en conjunto y así lo uniformice.

La fitogeografía de *Inga* en Mesoamérica muestra un importante elemento endémico de 33 especies (41.25%) incluyendo al área fitogeográfica del norte, o sea el sur de Veracruz y la zona de Tuxtepec en Oaxaca; si a ella agregamos la otra área natural al Sur, es decir la zona del Chocó colombiano y ecuatoriano, sumariamos 11 especies más o sea un total de 44 especies que representan el 55% de las Ingas del área.

Los otros elementos importantes son las 12 especies amazonicas (15%); las cinco de la flora de México (6.25%); las siete del arco que forma un brazo Colombia-Guayanas y el otro Colombia-Bolivia (8.7%), generalmente en áreas montañosas; las cuatro Colombia-Venezuela y en ocasiones Trinidad (5%); y otros modelos de distribución más amplia que sólo representan a ocho especies o sea el 10% de las Ingas.

Para este análisis estamos considerando a 80 especies, ya que *Inga edulis* muy probablemente se trata de una especie introducida al área mesoamericana.

Del elemento endémico, nueve especies (26.47%) son del área de bajas altitudes de la vertiente del Golfo de México; de las áreas montañosas, cinco especies (14.5%) corresponden a Chiapas–Honduras y siete especies (20.58%) a la de Nicaragua–Panamá, estando las siete presentes en Costa Rica; de las áreas de baja altitud, hay dos especies (5.88%) de Veracruz–Oaxaca a Costa Rica–Panamá, dos especies (5.88%) endémicas a Costa Rica, tres especies (8.82%) a Costa Rica–Panamá, y seis especies (17.65%) sólo de Panamá.

**Inga** Miller Gard. Dict. Abr., ed. 4, 2. 1754.

Arboles inermes; ramas teretes a tetragonales, glabras a pelosas. Hojas alternas, estipuladas, 1-pinnadas, paripinnadas, 1–14-yugadas, los folíolos opuestos; raquis teretes a alados, con glándulas interfoliolares, frecuentemente rematando en un apéndice. Inflorescencias generalmente axilares en fascículos o paniculadas en ramas áfilas, las flores uniformes, en racimos, espigas, capítulos o umbelas; brácteas florales homomorfas a heteromorfas, fértiles a estériles. Flores sésiles a largamente pediceladas; cáliz sinsépalo, campanulado a tubular, con o sin escotaduras, 5-lobado, en botón abierto a cerrado; corola simpétala, tubular, subturbinada a turbinada, 5-lobada, pelosa; estambres numerosos, monadelfos, con el tubo exerto a inserto, las anteras eglandulares; el polen en poliadras; gineceo 1-carpelar, el ovario multiovular; estilo más largo que los estambres, el estigma simple o lobado. Legumbre aplanada, tetragonal o subterete, derecha, curveada, helicoidal a circinado-espiralada, coriácea a leñosa, glabra a pelosa, las valvas en ocasiones reducidas y entonces los márgenes hipertrofiados; irregularmente dehiscente; semillas carnosas, oblongas, desnudas o en ocasiones cubiertas por una delgada testa papirácea que a su vez está cubierta por un tejido endocárpico suculento que ha sido interpretado como arilo, sin línea fisural; cotiledones bien desarrollados, la germinación frecuentemente ocurre en el fruto. Aprox. 350 spp. Trópicos y subtrópicos húmedos de América.

GRUPOS

1a. Inflorescencias racemosas o espigadas.
2a. Cáliz campanulado a brevemente tubular.
3a. Cáliz 1–1.5 mm; legumbre glabrescente a glabra. ..... GRUPO 1
3b. Cáliz 3–6 mm; legumbre densamente pelosa. ..... GRUPO 5
2b. Cáliz tubular a ciatiforme.
4a. Legumbres aplanadas a tetragonales.
5a. Lóbulos del cáliz triangulares a obtusos.
6a. Legumbres maduras glabras a pelosas, pero no tan densamente que impida ver el color o nervación de las valvas, con indumento más o menos rígido.
7a. Cáliz 2–5 mm, generalmente sin escotaduras, en botón obtuso. ..... GRUPO 2
7b. Cáliz 5–15 mm, generalmente con escotaduras, en botón obtuso o apiculado a rostrado. ..... GRUPO 3
6b. Legumbres maduras con pelosidad densa que da el color al fruto, generalmente hirsutas. ..... GRUPO 4
5b. Lóbulos del cáliz cuspidados a caudados. ..... GRUPO 6
4b. Legumbres subteretes, acordonadas. ..... GRUPO 7
1b. Inflorescencias capituliformes o umbeliformes.
8a. Inflorescencias capituliformes, con flores sésiles o pediceladas, los pedicelos hasta 3 veces la longitud del cáliz. ..... GRUPO 8
8b. Inflorescencias umbeliformes, los pedicelos de más de 3 veces la longitud del cáliz. ..... GRUPO 9

GRUPO 1

Flores pequeñas, cáliz 1–1.5 mm, campanulado a brevemente tubular; legumbres aplanadas, glabrescentes a glabras.

1a. Raquis floral largo, más de 2.5 cm.
2a. Valvas de la legumbre aplanadas.
3a. Corola ligeramente infundibuliforme, pelosa, tubo estaminal inserto o cortamente exerto. ..... *I. longispica*
3b. Corola tubular-campanulada, generalmente glabra, tubo estaminal largamente exerto (en el Continente Americano, inserto en las Antillas). ..... *I. laurina*
2b. Valvas de la legumbre abolladas o con proyecciones cónicas a la altura de las semillas.
4a. Legumbre lisa, abollada a la altura de las semillas.
5a. Folíolos hasta 12 cm de ancho; raquis foliar terete a marginado; brácteas florales triangular-obtusas. ..... *I. coruscans*
5b. Folíolos hasta 5 cm de ancho; raquis foliar marginado a alado; brácteas florales aleznadas. ..... *I. semialata*
4b. Legumbre verrugosa, con proyecciones cónicas a la altura de las semillas. ..... *I. riopalenquensis*
1b. Raquis floral corto, hasta 2.5 cm.
6a. Flores sésiles o casi sésiles.
7a. Pedúnculos florales más de 1.5 cm; tubo estaminal menos de 1.5 veces más largo que la corola; árboles generalmente menos de 20 m.
8a. Glándulas interfoliolares urceoladas, el cuerpo glandular 0.7–1.0 × 0.7–1.0 mm; legumbre hasta 2.3 cm de ancho, las valvas aplanadas a la altura de las semillas. ..... *I. belizensis*
8b. Glándulas interfoliolares cupuliformes, el cuerpo glandular 1.5–2.1 × 1.5–2.1 mm; legumbre hasta 3.2 cm de ancho, las valvas abolladas a la altura de las semillas. ..... *I. pezizifera*
7b. Pedúnculos florales hasta 1.1 cm; tubo estaminal 2 veces o más largo que la corola; árboles generalmente más de 25 m. ..... *I. alba*
6b. Flores largamente pediceladas. ..... *I. heterophylla*

GRUPO 2

Cáliz 2–5 mm, generalmente sin escotaduras, en botón obtuso.

1a. Brácteas florales heteromorfas, las distales cuculado-estipitadas, las proximales ovadas a obovadas, oblongas o triangulares.
2a. Raquis foliar terete a marginado; pelosidad de las ramas esparcida.
3a. Hojas (4–)6(–8)-folioladas. ..... *I. acrocephala*
3b. Hojas 10–12-folioladas.
4a. Folíolos simétricos a ligeramente asimétricos; valvas de la legumbre glabras o casi glabras, sin escamas. ..... *I. ruiziana*
4b. Folíolos marcadamente asimétricos en la base; valvas de la legumbre escuamosas. ..... *I. samanensis*
2b. Raquis foliar alado; pelosidad de las ramas densa. ..... *I. hintonii*
1b. Brácteas florales homomorfas, lanceoladas, linear-lanceoladas o triangulares.
5a. Flores proximales sésiles.

6a. Raquis foliar terete. ..... *I. punctata*
6b. Raquis foliar marginado a alado.
7a. Corola de 3–4.5 veces más larga que el cáliz. ..... *I. stenophylla*
7b. Corola hasta 2.5 veces más larga que el cáliz.
8a. Cáliz 1.6–2.2 mm; legumbre hasta 1.6 cm de ancho. ..... *I. tenuipedunculata*
8b. Cáliz 2.5–5 mm; legumbre hasta 4.8 cm de ancho. ..... *I. densiflora*
5b. Flores proximales pediceladas.
9a. Raquis foliar glabro, las glándulas interfoliolares ca. 3 mm de diámetro, escuteladas; cáliz glabrescente; legumbre hasta 4 cm de ancho, glabra. ..... *I. latipes*
9b. Raquis foliar velutino con tricomas pardo-amarillentos, las glándulas interfoliolares ca. 1 mm de diámetro, cupuliformes; cáliz peloso; legumbre hasta 2.6 cm de ancho, pelosa. .. *I. pinetorum*

Grupo 3

Cáliz 5–15 mm, tubular, generalmente con escotaduras, en botón obtuso o apiculado a rostrado.

1a. Hojas 2–6-folioladas.
2a. Legumbres glabras.
3a. Legumbres hasta 2.5 cm de ancho; cáliz en botón largamente rostrado. ..... *I. acuminata*
3b. Legumbres 3.5–6 cm de ancho; cáliz en botón apiculado, obtuso a largamente rostrado.
4a. Raquis foliar generalmente terete; ramas jóvenes teretes. ..... *I. leiocalycina*
4b. Raquis foliar angulado a cuadrangular o marginado a alado; ramas jóvenes anguladas a cuadrangulares.
5a. Hojas 6-folioladas; folíolos acuminados; flores amarillas.
6a. Ramas jóvenes y nervaduras primarias tomentosas con tricomas pardo-amarillentos; folíolos hasta 11 cm de ancho; glándula en el acumen foliolar ocasionalmente presente. ..... *I. urabensis*
6b. Ramas jóvenes y nervaduras primarias glabras; folíolos hasta 7 cm de ancho; glándula en el acumen foliolar frecuentemente presente. ..... *I. venusta*
5b. Hojas 4-folioladas; folíolos obtusos a apiculados; flores blancas. ..... *I. spectabilis*
2b. Legumbres pelosas, con tricomas más o menos rígidos.
7a. Inflorescencias largas y laxas, las flores espaciadas en el raquis. ..... *I. dwyeri*
7b. Inflorescencias cortas y compactas, las flores congestas en el raquis. ..... *I. hayesii*
1b. Hojas 8–18-folioladas.
8a. Raquis floral hasta 9 cm. ..... *I. skutchii*
8b. Raquis floral hasta 3.5 cm.
9a. Glándulas interfoliolares largamente estipitadas. ..... *I. ciliata*
9b. Glándulas interfoliolarees sésiles a casi sésiles.
10a. Valvas de las legumbres maduras glabras.
11a. Hojas (10–)12–22-folioladas; corola 20–25 mm; legumbre hasta 4.6 cm de ancho. ..... *I. multijuga*
11b. Hojas 8–12(–14)–folioladas; corola 12–18 mm; legumbre hasta 2.5 cm de ancho. ..... *I. aestuarorium*
10b. Valvas de las legumbres maduras pelosas.
12a. Corola 16–29 mm; legumbres estrigulosas.
13a. Folíolos concoloros a ligeramente discoloros; glándulas interfoliolares más pequeñas que el raquis foliar; flores robustas; cáliz 11–15 mm. ..... *I. cuspidata*
13b. Folíolos marcadamente discoloros; glándulas interfoliolares tan anchas o más anchas que el raquis foliar; flores esbeltas; cáliz 3–5 mm. ..... *I. thibaudiana*
12b. Corola 7–11 mm; legumbres hispídulas.
14a. Corola 9–11 mm; brácteas 1–1.7 mm; botones florales obtusos. ..... *I. micheliana*
14b. Corola 7–8 mm; brácteas 3–9 mm; botones florales rostrados a apiculados. ..... *I. flexuosa*

Grupo 4

Legumbres maduras con pelosidad densa que da el color al fruto, generalmente hirsutas.

1a. Glándulas interfoliolares generalmente largamente estipitadas.
2a. Raquis foliar terete. ..... *I. exalata*
2b. Raquis foliar alado.
3a. Flores esbeltas.
4a. Cáliz más de 10 mm; brácteas tan largas o más largas que el cáliz, persistentes.
5a. Pelosidad de tallos, ejes foliares y florales hirsuta; estípulas ovadas a triangular-cordatas, persistentes; brácteas generalmente lanceoladas.
6a. Hojas 2–4-folioladas; corola 15–18 mm. ..... *I. jimenezii*
6b. Hojas (4–)6–10-folioladas; corola 20–27 mm. ..... *I. tonduzii*

5b. Pelosidad de tallos, ejes foliares y florales tomentosa; estípulas filiformes a triangular-atenuadas, pronto caducas; brácteas filiformes a oblanceoladas. ____ *I. calderonii*

4b. Cáliz menos de 10 mm; brácteas generalmente menos del ½ de largo del cáliz, caducas.

7a. Cáliz inconspicuamente estriado o totalmente cubierto de indumento; brácteas ovadas a triangulares.

8a. Hojas 6-folioladas; folíolos cartáceos. ____ *I. litoralis*

8b. Hojas 8–12-folioladas; folíolos coriáceos. ____ *I. herrerae*

7b. Cáliz conspicuamente estriado; brácteas oblongas a lineares. ____ *I. tenella*

3b. Flores robustas.

9a. Estípulas cordatas, tan anchas como largas; glándulas sobre las nervaduras medias de los folíolos frecuentemente presentes; inflorescencias multifloras (10–22); corola 24–28 mm. ____ *I. goldmannii*

9b. Estípulas no cordatas, más largas que anchas; glándulas sobre las nervaduras medias de los folíolos ausentes; inflorescencias paucifloras (3–4); corola 28–32 mm. ____ *I. davidsei*

1b. Glándulas interfoliolares sésiles a casi sésiles.

10a. Glándulas sobre las nervaduras medias de los folíolos frecuentemente presentes; folíolos cocleados.

11a. Raquis foliar marginado a generalmente alado; brácteas 6–9 mm. ____ *I. sierrae*

11b. Raquis foliar terete; brácteas ca. 2 mm. ____ *I. cabrerae*

10b. Glándulas sobre las nervaduras medias de los folíolos ausentes; folíolos más o menos aplanados.

12a. Cáliz conspicuamente estriado.

13a. Cáliz glabro excepto en el ápice; corola 35–55 mm. ____ *I. mucuna*

13b. Cáliz peloso en toda su longitud; corola hasta 25 mm.

14a. Pecíolo 4.5–8.5 cm; legumbre hasta 18.5 cm, hirsuta con tricomas ferrugíneos; corola blanca. ____ *I. leonis*

14b. Pecíolo 1–3.5 cm; legumbre hasta 12 cm, hirsuta con tricomas pardo-amarillentos; corola verdosa. ____ *I. chiapensis*

12b. Cáliz sin estriaciones o si las tiene cubiertas por el indumento.

15a. Corola 14–15 mm, subturbinada; raquis foliar terete. ____ *I. cabrerae*

15b. Corola 21 mm o más, tubular; raquis foliar terete o marginado a alado.

16a. Flores proximales sésiles; legumbre hasta 5 cm de ancho. ____ *I. sinacae*

16b. Flores proximales pediceladas; legumbre hasta 2.7 cm de ancho. ____ *I. calcicola*

### Grupo 5

Cáliz 3–6 mm, robusto, campanulado. ____ *I. rubiginosa*

### Grupo 6

Raquis foliar alado; lóbulos del cáliz cuspidados a caudados, cáliz abierto en botón; legumbres aplanadas a tetragonales.

1a. Corola 18–30 mm; legumbres 11–30 × 2–3.5 cm.

2a. Flores proximales pediceladas; cáliz 16–21 mm; legumbre aplanada; tallos jóvenes con tricomas hasta 3 mm. ____ *I. ismaelis*

2b. Flores proximales sésiles; cáliz 9–17 mm; legumbre tetragonal; tallos jóvenes con tricomas hasta 1 mm. ____ *I. pavoniana*

1b. Corola 10–15 mm; legumbres 3.9–7.6 × 1.8–3.2 cm.

3a. Tallos y ejes foliares glabros; estípulas triangular-subuladas; glándulas interfoliolares sésiles. ____ *I. lacustris*

3b. Tallos y ejes foliares híspidos; estípulas setiformes, arqueadas; glándulas interfoliolares largamente estipitadas. ____ *I. cookii*

### Grupo 7

Legumbres subteretes, acordonadas.

1a. Raquis foliar terete.

2a. Hojas (4–)6–8(–10)-folioladas. ____ *I. oerstediana*

2b. Hojas (10 )12 16-folioladas. ____ *I. cocleensis*

1b. Raquis foliar alado.

3a. Glándulas interfoliolares urceoladas a pateniformes, el ósculo circular, generalmente hasta 1.2 mm de diámetro.

4a. Legumbres con los márgenes parcialmente hipertrofiados, las valvas reducidas pero aún claramente se distinguen.

5a. Flores proximales sésiles; cáliz 6 10 mm, tubular, esbelto; corola hasta 20 mm, generalmente el doble de la longitud del cáliz. ____ *I. affinis*

5b. Flores proximales frecuentemente pediceladas; cáliz 10–18 mm, infundibuliforme, robusto; corola hasta 25 mm, menos del doble de la longitud del cáliz. ____ *I. vera*

4b. Legumbres con los márgenes totalmente hipertrofiados, las valvas difícilmente distinguibles de los márgenes; flores proximales sésiles.

6a. Hojas (4–)6–8-folioladas; brácteas hasta 2.3 mm; legumbre hasta 2.2 cm de diámetro. ..... *I. pauciflora*
6b. Hojas 4-folioladas; brácteas hasta 11 mm; legumbre hasta 3.5 cm de diámetro. ..... *I. chocoensis*

3b. Glándulas interfoliolares pateniformes, el ósculo transversalmente oval u oval alargado a frecuentemente lunular, generalmente más de 2 mm de diámetro.
7a. Hojas (4–)6–8(–10)-folioladas; brácteas caducas; legumbre 8–32 × 1.2–1.5 cm, los márgenes parcialmente hipertrofiados, las valvas reducidas pero distinguibles.
8a. Brácteas 1–4 mm, reniformes a ovales. ..... *I. oerstediana*
8b. Brácteas 7–15 mm, oval-oblongas, oblanceoladas. ..... *I. latibracteata*
7b. Hojas 8–12-folioladas; brácteas más o menos persistentes; legumbre 40–150 × 2–3.5 cm, los márgenes totalmente hipertrofiados, las valvas indistinguibles de los márgenes. ..... *I. edulis*

Grupo 8

Inflorescencias capituliformes, con flores sésiles a pediceladas, los pedicelos hasta 3 veces la longitud del cáliz.

1a. Raquis foliar marginado a alado.
2a. Organos vegetativos y legumbres pelosas.
3a. Hojas 4–6-folioladas; flores densamente pelosas; legumbre 4–6.5 cm de ancho. ..... *I. dasycarpa*
3b. Hojas 6–10-folioladas; flores glabras, excepto los lóbulos de la corola; legumbre 1.8–2 cm de ancho. ..... *I. pseudoinvolucrata*
2b. Organos vegetativos y legumbres glabrescentes a glabras.
4a. Raquis foliar marginado, las glándulas interfoliolares piriformes, largamente estipitadas; corola 5–7 mm. ..... *I. allenii*
4b. Raquis foliar alado, las glándulas interfoliolares pateniformes a cupuliformes, sésiles a casi sésiles; corola 20–50 mm.
5a. Cáliz 13–14 mm; corola 20–23 mm, densamente setosa con tricomas pardo-amarillentos en el ⅓ superior; tubo estaminal inserto a cortamente exerto. ..... *I. portobellensis*
5b. Cáliz 24–33 mm, corola 38–50 mm, glabra excepto sericea con tricomas canescentes en el ápice de los lóbulos; tubo estaminal largamente exerto. ..... *I. bella*

1b. Raquis foliar terete.
6a. Estípulas pronto caducas.
7a. Corola pelosa en toda su longitud.
8a. Ramas e inflorescencias tomentosas. ..... *I. quaternata*
8b. Ramas e inflorescencias glabrescentes a glabras.
9a. Cáliz 1.5–3 mm; corola 6–9 mm, la corola 2.2–3.5 veces la longitud del cáliz. ..... *I. acrocephala*
9b. Cáliz 5–7 mm; corola 9–12 mm, la corola hasta 2 veces la longitud del cáliz. ..... *I. mortoniana*
7b. Corola glabra excepto pelosa sobre los lóbulos.
10a. Pedúnculo 0.5–1.5 cm; cáliz 1.2–1.5 mm; corola 6–7 mm; legumbre ca. 7 × 2.5–3 cm, circinado-espiralada. ..... *I. glomeriflora*
10b. Pedúnculo (1–)3–6 cm; cáliz 1.5–2 mm; corola 4–6 mm; legumbre 15–50 × 3.5–5 cm, linear-oblonga. ..... *I. jinicuil*
6b. Estípulas persistentes.
11a. Estípulas oblongas a obovadas.
12a. Cáliz aplicado a la corola; corola 4–7.5 mm. ..... *I. paterno*
12b. Cáliz amplio no aplicado a la corola; corola 17–25 mm.
13a. Hojas 2–4-folioladas; legumbre linear-oblonga. ..... *I. cordistipula*
13b. Hojas 6–8-folioladas; legumbre circinado-espiralada. ..... *I. spiralis*
11b. Estípulas aciculares; lóbulos del cáliz filiformes a lanceolado-aleznados.
14a. Tallos y ejes foliares glabrescentes; glándulas interfoliolares sésiles; legumbre glabra, verrugoso-lenticelada. ..... *I. filiformis*
14b. Tallos y ejes foliares setosos; glándulas interfoliolares largamente estipitadas; legumbre largamente pelosa, sin lenticelas. ..... *I. saffordiana*

Grupo 9

Inflorescencias umbeliformes, los pedicelos más de 3 veces la longitud del cáliz.
1a. Hojas 8–12-folioladas. ..... *I. flagelliformis*
1b. Hojas generalmente 2–6-folioladas.
2a. Estípulas aleznadas; brácteas 1.2–1.4 mm. ..... *I. sertulifera*
2b. Estípulas lanceoladas u oblanceoladas a linear-lanceoladas; brácteas 2–9 mm.
3a. Hojas (2–)4–6-folioladas; pedúnculo floral 2 3 cm; brácteas hasta 5 mm, oblanceoladas. ..... *I. umbellifera*
3b. Hojas 2(–4)-folioladas; pedúnculo floral hasta 1 cm; brácteas hasta 9 mm, lanceoladas a linear-lanceoladas. ..... *I. polita*

**Inga acrocephala** Steudel, Flora 26: 759. 1843. TIPO: Surinam: *Hostmann 1067* (isotipos, BM, F, K, MO).

*Inga brevipedicellata* Harms, Repert. Spec. Nov. Regni Veg. 19: 62. 1923. TIPO: *J. A. Purpus 282* (holotipo, B destruido).

*Inga brevipedicellata* se había mantenido como una especie del sur de México y del norte de Centroamérica, pero han empezado a aparecer ejemplares de Costa Rica y Panamá que extendieron su distribución (Zamora, anotación de ejemplares, com. pers.). También con las nuevas colectas la variación se ha ampliado y así tenemos ejemplares de Veracruz francamente pedicelados y los de Chiapas, hacia el sur, sésiles. En Sudamérica en Colombia y Ecuador las hojas se mantienen con seis folíolos, pero en el área de las Guayanas tenemos hojas 8-folioladas, único carácter que podría mantener separada a *I. brevipedicellata* de *I. acrocephala*.

Sobre el tipo de *Inga brevipedicellata* que designó Harms (1923), *J. A. Purpus 282* del Herbario de Berlin (B), fué destruido y el único aparente duplicado que he visto está en el Smithsonian (US, 1202084): se trata de un ejemplar en flor que muestra claramente las flores sésiles a casi sésiles, las brácteas homomorfas linear-lanceoladas además de hojas 4–6-folioladas características de *Inga punctata* Willd.; además, existe el ejemplar de *J. A. Purpus 281* (G), el cual está correctamente identificado como *I. leptoloba* Schldl. [*I. punctata* Willd.], por lo que debe haber habido una confusión de etiquetas.

Por otro lado, por el momento, mantenemos separada a *Inga acrocephala* de *I. acreana* Harms (véase también *I. allenii*), no por los razonamientos, descripción, y ejemplares citados por Poncy (1985), ni por las observaciones de Macbride (1943) respecto al raquis foliar, sino por el cáliz de mayor tamaño de *I. acreana* Harms. Otro aspecto de variación en *I. acrocephala* es la transición de tipos de inflorescencias (que en ocasiones ocurren en el mismo ejemplar (*Ibarra M. 470*, MEXU)) de racimos cortos a capítulos, y de hecho debilita enormemente la taxonomía actual de secciones definidas por tipos de inflorescencias.

*Material representativo.* MEXICO. CHIAPAS: *Téllez V. 646* (MEXU). VERACRUZ: *Sousa 3044* (MEXU). GUATEMALA. EL PETEN: *Contreras 9474* (LL). IZABAL: *Tenorio et al. 14518* (MEXU). HONDURAS. ATLANTIDA: *Molina R. 10493* (F). COSTA RICA. ALAJUELA: *Jiménez 1768* (F). HEREDIA: *Schubert & Holdridge 1353* (A). LIMON: *Hammel & Grayum 14340* (NY). PUNTARENAS: *Kennedy 2009* (MO). PANAMA. COLON: *Crosby & Denslow 6480* (MO). DARIEN: *Croat 68964* (MO). PANAMA: *Dressler 3272* (MEXU). VERAGUAS: *Croat 27696* (MO). COLOMBIA. ANTIOQUIA: *Rentería et al. 2837* (MO). CUNDINAMARCA: *Gentry & Fallen 17125* (MO). CHOCO: *Gentry et al. 37072* (MO). SURINAM: *Hostmann 1067* (MO). GUAYANA FRANCESA: *Wachenheim 312* (US). ECUADOR: *Palacios et al. 465* (MO). BRASIL. (NORTE) AMAPA: *Maguire et al. 47112* (K).

**Inga acuminata** Benth., London J. Bot. 4: 600. 1845. TIPO: Trinidad: *Lockhart 334* (holotipo, K).

Esta especie hasta hace poco ha sido colectada en Mesoamérica. Muy característica por sus botones florales con el cáliz cerrado largamente rostrado.

*Material representativo.* COSTA RICA. HEREDIA: *Opler 1593* (F). PANAMA. BOCAS DEL TORO: *McPherson & Aranda 10102* (MO). DARIEN: *Duke 4934* (MO). ZONA DEL CANAL: *Foster 2976* (MO). TRINIDAD: *Britton et al. 2575* (GH). COLOMBIA. CHOCO: *Gentry 9336* (MO). VENEZUELA. ZULIA: *Zambrano & Gutiérrez 1556* (MO). ECUADOR: *H. Eggers 15825* (K).

**Inga aestuariorum** Pittier, Contr. U.S. Natl. Herb. 18: 183, t. 89. 1916. TIPO: Costa Rica: *Tonduz 6793* (holotipo, US; isotipos, BR, G).

León (1966) incluye a *Inga aestuariorum* como sinónimo de *I. multijuga* Benth. (véase ésta), adoptando el concepto de Bentham (1875) y reconociendo que ésta "podría quizá ser una variante subespecífica," sugerencia que Bentham también consideró al incluir el ejemplar de Oersted de Costa Rica ("perhaps a variety with rather smaller flowers"). Sin embargo, en el norte del Istmo de Panamá las dos especies son simpátricas, y así Fendler en enero 24 de 1850 las colectó (en flor) en Chagres, única área que él visitó en su único viaje a Panamá (véase Stieber & Lange, 1986). Ambas especies fueron colectadas bajo el mismo número (51) de colecta, estando depositada *I. aestuariorum* en el GH e *I. multijuga* en K, MO, y US. *Inga aestuariorum* la mantengo separada considerando su menor número de folíolos por hoja, la flor más pequeña y el fruto que sólo llega hasta 2.5 cm de ancho. Es interesante agregar que el material de la vertiente del Golfo de México es muy homogéneo, distinguiendose por sus glándulas interfoliolares del raquis foliar característicamente con el ósculo muy cerrado, siendo transversalmente linear-oblongo; en cambio en el material de Nicaragua a Panamá, el ósculo es más o menos circular.

*Material representativo.* MEXICO. CHIAPAS: *Breedlove 34962* (MO). OAXACA: *Sousa et al. 13101* (MEXU). VERACRUZ: *Sousa 3085* (MEXU). GUATEMALA. ALTA VERAPAZ: *Standley 90278* (F). EL PETEN: *Tún Ortíz 1084*

(BM). NICARAGUA. RIO SAN JUAN: *Grijalva & Almanza 3606* (MO). COSTA RICA. PUNTARENAS: *Burger & Liesner 6702* (F). PANAMA. CHIRIQUI: *Croat 21906* (MO). HERRERA: *Carrasquilla & Lao 347* (MO). VERAGUAS: *Allen 154* (MO).

**Inga affinis** DC., Prodr. 2: 433, 1825. TIPO: Brasil: *Raddi s.n.* (holotipo, G-DC, foto MO).

Especie muy relacionada con *Inga vera* Willd. e *I. uraguensis* Hook. et Arn. ["*uruguensis*"]; de la primera difiere *I. affinis* por contar con flores sésiles o casi sésiles, un cáliz más pequeño (6–10 mm), tubular y la corola generalmente el doble del cáliz. De *I. uruguensis*, las diferencias son más tenues, ya que ambas cuentan con flores del mismo tamaño y la diferencia fundamental está en la mayor relación de la longitud del cáliz con respecto a la corola; en *I. uruguensis* la corola es solamente 1.5 vez más larga que el cáliz. Por lo anterior sin grandes problemas *I. uruguensis* podría pasar como sinónimo de *I. affinis*.

En Mesoamérica esta especie había sido interpretada como *Inga edulis* C. Martius o bien *I. vera* Willd.; de la primera, a pesar de contar con flores de similar tamaño y proporción, difiere por las glándulas interfoliolares más pequeñas y el fruto de menor tamaño con las valvas angostas pero aun visibles, caracteres que la acercan más a *I. vera*.

*Material representativo.* MEXICO. CAMPECHE: *Ramírez R. & Flores C. 97* (MEXU). CHIAPAS: *Martínez S. & Aguilar 12368* (MEXU). OAXACA: *Sousa et al. 13104* (MEXU). SAN LUIS POTOSI: *Fryxell & Anderson 3425* (F). TABASCO: *Orozco S. & González 26* (MEXU). VERACRUZ: *Palmer 362* (MO). BELICE. BELICE: *Dwyer 13096* (MO). GUATEMALA. EL PETEN: *Contreras 7719* (MEXU). HONDURAS. OLANCHO: *Ortega U. 210* (MO). NICARAGUA. CHONTALES: *Vincelli 125* (MEXU). ZELAYA: *Stevens 10460* (MO). COSTA RICA. LIMON: *Davidse & Herrera 30907* (MO). PANAMA. PANAMA: *Muñoz 47* (MO). COLOMBIA. CASANARE: *Uribe U. 5584* (F). VENEZUELA. APURE: *Davidse & González 14354* (MO). BOLIVAR: *Ll. Williams 11615* (MO). ECUADOR. GUAYAS: *Harling & Anderson 19342* (MO). PERU. CUZCO: *C. Vargas C. 13668* (MO). MADRE DE DIOS: *Gentry et al. 26946* (MO). BRASIL. (NORTE) PARA: *Plowman et al. 9904* (MO). (NORESTE) BAHIA: *Glocker 593* (MO). PERNAMBUCO: *Gardner 1838* (US). (CENTRO OESTE) DISTRITO FEDERAL: *Irwin et al. 11421* (MO). GOIAS: *Prance & Silva 59533* (MO). MATO GROSSO: *Pirani 1163* (MO). (SUDESTE) SÃO PAULO: *Eiten & Clayton 6078* (MO). (SUR) RIO GRANDE DO SUL: *Hagelud 12270* (F). ARGENTINA. CORRIENTES: *Seigler et al. DS-10147* (MO). CHACO: *Charpin & Eskuche AC20146* (MO). PARAGUAY: *Morong 528* (MO). URUGUAY: *Bernardi 18680* (MO).

**Inga alba** (Sw.) Willd., Sp. Pl. ed. 4, 4: 1013. 1806. Basiónimo: *Mimosa alba* Sw., Prodr. 85. 1788, non M. Vahl, 1807. TIPO: Guayana Francesa: *von Rohr s.n.* (fl) (lectotipo, designado aquí, BM).

Sobre la lectotipificación de *Inga* y su basiónimo *Mimosa alba* Sw., el mismo O. Swartz (1788) nos informa que se trata del material de "Cayenna," y al estar marcada la descripción de la especie por un pequeño sol similar a un asterisco, el material lo consultó en el Herb. de J. Banks (BM) como el mismo Swartz refiere en su prefacio, sin anotar al colector. Por otro lado Poncy (1985) refiere al ejemplar de *von Rohr* como el tipo de este nombre de Cayenne en el BM, sin lectotipificarlo, así que aquí sólo se está formalizando lo que Poncy apuntó, y yo concuerdo. Existe un ejemplar en flor, anotado como *Mimosa alba* Sw. de Cayenne y colectado por *von Rohr s.n.* (BM).

Especie que alcanza las mayores tallas en el género (hasta 40 m), con flores e inflorescencias inconspicuas, lo que ha contribuido a su escasa representación en herbarios. Sin embargo, existen varios ejemplares estériles, que hacen suponer su aparente frecuencia en el dosel de las selvas altas perennifolias de América cálido húmeda.

*Inga alba* está estrechamente relacionada a *I. lateriflora* Miq. de la sección *Leptinga* Benth. difiriendo fundamentalmente por el tipo de inflorescencia; esta afinidad debilita los límites de las secciones *Bourgonia* Benth. y *Leptinga* Benth.

Esta especie en Mesoamérica ha sido confundida con *Inga fagifolia* (L.) Willd. ex Benth. (*I. laurina* (Sw.) Willd.).

*Material representativo.* MEXICO. OAXACA: *Hernández G. 2495* (MEXU). VERACRUZ: *Wendt et al. s.n.* (MEXU). NICARAGUA. ZELAYA: *Proctor et al. 27032* (NY). COSTA RICA. HEREDIA: *Hammel 11662* (MO). PUNTARENAS: *Holdridge 5275* (F). PANAMA. SAN BLAS: *de Nevers et al. 7563* (MO). ZONA DEL CANAL: *Wetmore & Abbe 129* (F). COLOMBIA. VAUPES: *A. S. Barclay & R.E. Schultes 509* (K). VENEZUELA. AMAZONAS: *Colchester 2423* (K). BOLIVAR: *Steyermark 60417* (MO). DELTA AMACURO: *Blanco 171* (MO). MERIDA: *Breteler 4756* (U). GUYANA: *Maas & Westra 3901* (MO). SURINAM: *B. W. [Sur. For. Dept.] 6174* (MO). GUAYANA FRANCESA: *Prévost & Grenand 973* (MO). ECUADOR. NAPO: *Neill et al. 8292* (MO). PERU. LORETO: *Vásquez & Jaramillo 1178* (MO). BOLIVIA: Bang Lectae 1439 (MO). BRASIL. (NORTE) AMAPA: *Robelo et al. 2280* (MO). AMAZONIA: *Krukoff 6603* (MO). PARA: *Silva & Souza 2355* (MO). RONDONIA: *Cid et al. 4942* (MO). RORAIMA: *Milliken & R. Miller 777* (K).

**Inga allenii** León, Ann. Missouri Bot. Gard. 53: 346. 1966. TIPO: Panamá: *Allen 2687* (holotipo, US).

Especie muy característica por sus glándulas interfoliolares piriformes largamente estipitadas. *Inga allenii* en general está relacionada a *I. mor-*

*toniana* León, como ya León (1966) lo había apuntado, pero la encuentro más cercana a *I. acreana* Harms (incluyendo a *I. myriocephala* Pittier) del área suroeste del Amazonas, de la cual es difícil separar, posiblemente siendo *I. allenii* una variedad de *I. acreana*.

*Material representativo.* COSTA RICA. HEREDIA: *Gómez P. et al. 21111* (MO). LIMON: *Grayum et al. 3502* (MO). PUNTARENAS: *Utley & Utley 1201* (F). PANAMA. COCLE: *Ebinger 965* (GH).

**Inga belizensis** Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 307. 1929. TIPO: Belice: *Schipp 24* (holotipo, F; isotipos, BM, K, MO, US).

Como ya apunto León (1966) esta especie está cercanamente relacionada a *Inga fagifolia* (L.) Willd. ex Benth. (*I. lauriana* (Sw.) Willd.); sin embargo se trata de dos especies aparte, no sólo por la inflorescencia sino también por el fruto (véase clave).

*Material representativo.* MEXICO. CHIAPAS: *Martínez S. 8517* (MEXU). BELICE. EL CAYO: *Lundell 6599* (NY). STANN CREEK: *Schipp 24* (MO). GUATEMALA. EL PETEN: *Lundell & Contreras 20841* (MEXU).

**Inga bella** M. Sousa, sp. nov. TIPO: Costa Rica. Puntarenas: Reserva Forestal Golfo Dulce, Osa Península, Rancho Quemado, ca. 15 km W of Rincón, in bottom of S end of valley along Río Riyito, 2 June 1988, *B. Hammel, G. Herrera, M. M. Chavarría & A. Solís 16962* (holotipo, MO; isotipos, CM, CR, MO).

*Inga portobellensis* auct. non Beurling. Ilustración: Pittier, Contr. U.S. Natl. Herb. 18: t. 83–84. 1916.

Similis *Ingae portobellensi* Beurling, a qua tamen inflorescentia pauciflora, calyce ac corolla duplo vel ultra longioribus, calyce laevi, corolla ex sparse canescenti-sericea glabrescenti, nec non tubo stamineo longe exserto differt.

Arboles 6–10 m; ramas subteretes, glabras. Hojas 4-folioladas; estípulas 7–24 mm, foliáceas, ovadas a ovado-lanceoladas, cordatas en la base, persistentes; pecíolo 1–4.5 cm, alado; folíolos concoloros, cartáceos a subcoriáceos, algo abollados, la base ligeramente asimétrica, cuneada, el ápice acuminado a cuspidado, el haz opaco, glabro, el envés opaco, glabro excepto esparcidamente seríceo sobre la nervadura primaria y secundarias, la nervadura primaria eglandular; par basal de folíolos 6–16 × (3–)5–7.5 cm, elípticos, o lanceolados a oblanceolados, el par apical 17–21 × 7–8.5 cm, elípticos a obovados; raquis foliar 4.5–7.5 cm, alado, el ala hasta 18 mm de ancho, oblanceolada a obtriangular; glándulas interfoliolares sésiles o casi sésiles, pateniformes a cupuliformes, el cuerpo glandular 2.5–3 × 2.5–3 mm; apéndice hasta 16 mm, caduco. Inflorescencias capituliformes, solitarias; pedúnculo 0.5–5.5 cm, aplanado, sulcado, glabro; raquis floral muy reducido, las brácteas gradualmente heteromorfas, 4–12 mm, foliáceas, ovadas a oblongas, las de la periferia de mayor talla, persistentes. Flores sésiles o brevipediceladas, los pedicelos hasta 5 mm, robustos; botones florales con el cáliz cubriendo, desconocidos; cáliz 24–33 mm, tubular-infundibuliforme, inflado, liso, glabro, sin escotaduras, los lóbulos 3–4 mm, ampliamente triangulares; corola 38–50 mm, tubular a subturbinada, blanco-verdosa, glabra excepto serícea con tricomas canescentes en el ápice de los lóbulos; tubo estaminal largamente exerto, blanco. Legumbre 18.5–22.5 × 2.6–3 × 0.4–0.7 cm, aplanada, curveada, linear-oblonga, sésil, rostrada en el ápice, esparcidamente puberulenta a glabra, las valvas transversal e inconspícuamente nervadas, las suturas, marginadas, los márgenes de las suturas aplanados.

*Distribución y hábitat.* De la vertiente pacífica de Costa Rica y Panamá; en Costa Rica solamente conocida en la Península de Osa y en Panamá, en el Darién. En altitudes de 5–250 m. Florece de abril a principios de junio, fructifica de abril a junio.

*Paratipos.* COSTA RICA. PUNTARENAS: Parque Nacional Corcovado, Sirena Station, 8°29′N, 83°34′O, *B. Hammel & C. Kernan 16656* (F, MO); Parque Nacional Corcovado, Sirena, Monkey Woods, 8°27′–30′N, 83°33′–38′O; *Kernan 363* (MO); Santo Domingo, Golfo Dulce, *Tonduz 9879* [colección base de la ilustración de Pittier] (BM, BR, F, GH, K, MEXU, MO, NY, US); Playa Blanca, Golfo Dulce, *M. Valerio 468* (F). PANAMA. DARIEN: Cana-Cuasi trail along Río Cuasi, *R. L. Hartman 12486* (MO); main stream of Río Cuasi, 0–2.5 mi. S of Tres Bocas, *J. H. Kirkbride & J. Duke 1132* (MO).

*Inga bella* está muy relacionada con *I. portobellensis* Beurling (sus diferencias son explicadas en la diagnosis, véase *I. portobellensis*); también se relaciona con *I. inflata* Ducke del Amazonas, pero *I. bella* difiere de esta última por las hojas de mayor talla y menos coriáceas, el raquis foliar alado, las estípulas bien desarrolladas y persistentes, las flores sésiles a casi sésiles, y la legumbre que es aplanada a la altura de las semillas. El epíteto hace resaltar la belleza de las hojas y flores de esta *Inga*, que potencialmente podría usarse como ornamental.

**Inga cabrerae** M. Sousa, sp. nov. TIPO: Guatemala. Baja Verapaz: Sierra de las Minas, 3 km SE of Purulhá, 2,000 m, 6 Jan. 1974,

*L. O. Williams, A. Molina R., T. P. Williams & A. R. de Molina 43415* (holotipo, F; isotipo, US).

Frutex vel arbor parva; ramis juvenilibus dense ferrugineo-tomentosis. Folia 3-jugata; stipulis 2–3 mm longis, ex ligulatis suborbiculatis; foliolis coriaceis, nervo medio glandulas interdum terentibus; rhachidi foliari tereti, glandulis interfoliolaribus sessilibus urceolatis. Inflorescentiae spiciformes; rhachidi florali 2–3.5 cm longa; bracteis homomorphis ca. 2 mm longis, late ligulatis. Flores sessiles; calyce ca. 6 mm longo, tubulari; corolla 14–15 mm longa, subturbinata, brunneo-lutescenti-villosa. Legumen usque ad 3 cm latum, lineari-oblongum, ex complanatum subtetragonale, ferrugineo-hirsutum.

Arbustos a árboles 2–6 m; ramas angulosas, ferrugíneo tomentosas cuando jóvenes, posteriormente glabrescentes. Hojas 6-folioladas; estípulas 2–3 mm, liguladas a suborbiculares, caducas; pecíolo 2–3 cm, terete; folíolos ligeramente discoloros, coriáceos, cocleados, la base simétrica, obtusa a aguda, el ápice generalmente apiculado a acuminado, en ocasiones obtuso, el haz brillante, esparcidamente piloso, tomentuloso sobre la nervadura primaria, el envés opaco, esparcidamente tomentuloso por la superficie, más densamente sobre las nervaduras, la nervadura primaria en ocasiones glandular proximalmente; par basal de folíolos 5.5–6.5 × 3.5–5 cm, ovados, el par apical 12–14 × 7–8.5 cm, anchamente elípticos; raquis foliar 6.5–8.5, terete; glándulas interfoliolares sésiles, urceoladas, el cuerpo glandular 1.5–2 × 1.5–2 mm, apéndice ca. 2 mm, grueso, caduco. Inflorescencias en espigas 1–2 fasciculadas; pedúnculo 1.5–3.5 cm, terete, inconspicuamente sulcado, ferrugíneo tomentoso; raquis floral 2–3.5 cm, las flores algo espaciadas proximalmente, congestas distalmente, las brácteas aparentemente homomorfas ca. 2 mm, anchamente ligualadas, caducas. Flores sésiles; botones florales con el cáliz abierto, los lóbulos erectos, obtusos; cáliz ca. 6 mm, tubular, sin estrías aparentes, tomentoso con tricomas pardo-amarillentos, sin escotaduras, los lóbulos ca. 1 mm, anchamente triangulares; corola 14–15 mm, subturbinada, blanca, vellosa con tricomas pardo-amarillentos; tubo estaminal inserto, blanco. Legumbre ca. 22 × 3 × 1 cm, aplanada, subtetragonal, curveada, linear-oblonga, atenuada en la base, apiculada en el ápice, ferrugíneo hirsuta, las valvas aplanadas, las suturas marginadas a acostilladas, las costillas hasta 4 mm de ancho, los márgenes de las suturas nervados.

*Distribución y hábitat.* Conocida del área de las Lagunas de Montebello, Chiapas, México, y de la Sierra de las Minas en Guatemala. En vegetación de transición entre selvas altas y bosques caducifolios, en bosques caducifolios con *Liquidambar* y en bosques de neblina. En altitudes entre los 1,600 y 2,000 m. Florece a principios de enero y fructifica en marzo.

*Paratipos.* MEXICO. CHIAPAS: Mpio. La Trinitaria, a 3 km al O de Tziscao, dentro de los límites del Parque Natural Lagos de Monte Bello, *E. Cabrera C. & H. de Cabrera 6063* (MEXU); a 15 km al E de las Lagunas de Monte Bello, *Cabrera C. et al. 1861* (MEXU, MO).

Especie muy cercana a *Inga dasycarpa* M. Sousa e *I. tenella* M. Sousa de las cuales se distingue fundamentalmente por su raquis foliar terete, sus glándulas interfoliolares sésiles urceoladas, con un cuerpo glandular de mayores dimensiones y la presencia de glándulas en la nervadura primaria. En cuanto a las inflorescencias *I. cabrerae* posee espigas, lo que la acerca más a *I. tenella*, pero el cáliz de este última es tubular-cónico, estriado y esparcidamente peloso. Es interesante anotar que estas tres especies se encuentran simpátricas en el área de las Lagunas de Montebello en Chiapas, estando aparentemente aisladas estacionalmente por floraciones en diferentes períodos; así *Inga cabrerae* florece en enero (aunque hay que aclarar que el dato es de Guatemala), *I. tenella* en marzo–abril, e *I. dasycarpa* en octubre.

Se dedica esta especie a Edgar Francisco Cabrera Cano (1957–), colector botánico del sur de México.

**Inga calcicola** M. Sousa, sp. nov. TIPO: México. Oaxaca. Curva del Diablo, a 4 km al ESE de Temazcal, en el camino al vertedero, Mpio. San Miguel Soyoltepec, Distr. Tuxtepec, 50 m, 30 jun. 1987, *M. Sousa S., G. Andrade, R. Torres C. & L. Cortés A. 13090* (holotipo, MEXU; isotipos, MEXU, MO). Figura 1.

Arbores medianae; folia (3–)4–5-jugata; rhachis foliaris anguste alata, glandulis interfoliolaribus diminutis, sessilibus vel fere sessilibus. Inflorescentiae racemosae corymboideae, pauciflorae; flores 21–27 mm longi, pedicellati vel sessiles; calyx ac corolla tubulares, tubo staminali inserto. Legumen lineari-oblongum angustum, brunneo-lutescenti-hirsutulum.

Arboles 3–12(–20) m; ramas teretes, velutinas con tricomas pardo-amarillentos cuando jóvenes, posteriormente glabrescentes. Hojas (6–)8–10-folioladas; estípulas 5 mm, liguladas a lanceoladas, caducas; pecíolo 1–2.5 cm, terete a marginado; folíolos ligeramente discoloros, cartáceos, la base ligeramente asimétrica, cuneada a obutsa, el ápice acuminado a cuspidado, el haz opaco, esparcidamente tomentoso, después glabrescente, las nervaduras tomentosas con tricomas pardo-amarillentos, el envés pálido con la misma pelosidad pero ésta más densa, la nervadura primaria eglan-

FIGURA 1. *Inga calcicola* M. Sousa. —A. Rama con inflorescencias.—B. Detalle de estípulas.—C. Glándula interfoliolar.—D. Botón floral.—E. Flor.—F. Cáliz.—G. Corola.—H. Tubo estaminal.—I. Gineceo. (Tomado de *Sousa 13090.*)—J. Fruto. (Tomado de *Sousa 10273.*)

dular; par basal de folíolos 3.5–8.5 × 2.1–4.2 cm, elíptico-lanceolados a ovados, el par apical 12.5–17(–19.5) × 4–6.5(–8.4) cm, elípticos en ocasiones obovados; raquis foliar 7–11(–20) cm, alado entre todos los pares de folíolos, el ala hasta 15 mm de ancho, oblanceolada; glándulas interfoliolares sésiles a subsésiles, urceoladas, el cuerpo glandular 0.8–1 × 0.8–1 mm; apéndice ausente. Inflorescencias racimos corimboides, 1–2 fasciculadas; pedúnculo 3.5–7 cm, subterete, sulcado, tomentoso con tricomas pardo-amarillentos; raquis floral 2–3 cm, las flores espaciadas proximalmente, congestas distalmente, las brácteas algo heteromorfas 3–4 mm, concavas, las proximales fre-

cuentemente estériles, ovadas en el ⅓ superior del pedúnculo, persistentes, las distales fértiles, espatuladas, persistentes. Flores proximales pediceladas, el pedicelo hasta 7 mm, las distales sésiles; botones florales con el cáliz cerrado, obtusos; cáliz 11–21 mm, tubular, estriado, tomentoso con tricomas pardo-amarillentos, sin escotaduras, los lóbulos 1–1.5 mm, triangular-obtusos; corola 21–27 mm, tubular, verde pálido, canescente sericea; tubo estaminal inserto, blanco. Legumbre 19–23.5 × 2–2.7 × 0.4–0.5 cm, aplanada, subespiralada a espiralada, linear-oblonga, sésil en la base, apiculada a rostrada en el ápice, hirsútula con tricomas pardo-amarillentos, las valvas aplanadas, las suturas derechas, los márgenes de las suturas aplanados.

*Distribución y hábitat.* Especie solamente conocida del norte de Oaxaca, en el distrito de Tuxtepec, en suelos de litosoles negros calizos. En selvas altas subperennifolias con *Brosimum* (Moraceae), como un elemento del estrato bajo arbóreo. En altitudes entre 30 y 130 m. Florece desde finales de mayo a la primera quincena de junio, la fructificación de septiembre a diciembre, con frutos en el suelo en febrero.

*Nombre vernáculo.* Guatope.

*Usos.* "Los frutos maduros son comestibles."

*Paratipos.* MEXICO. OAXACA: Distr. Tuxtepec, Mpio. San Miguel Soyaltepec, Presa de Temazcal, al NO sobre la cortina de la presa, *L. Cortés & R. Torres C. 3* (MEXU, MO); Isla Isabel Maria, cerca de San Miguel Soyaltepec, *Cortés & Torres 841* (MEXU); Temazcal, cerros cerca de los vertederos, a 7 km al SE de la cortina de la presa Miguel Alemán, *Martínez S. & L. Rico A. 6132, 6785* (MEXU); cortina de la Presa Alemán, Temazcal, *M. Sousa & L. Rico A. 10273* (MEXU); a 4 km al SE de Temazcal, camino a los vertederos de la presa, *Sousa e I. Calzada 13028, 13048, 13066* (MEXU, MO); enfrente de la caseta de vigilancia de los vertederos de la presa Miguel Alemán, Temazcal, *R. Torres & E. Cabrera 6151* (MEXU); Mpio. Santa Maria Jacatepec, El Aguila, La Joya del Obispo, *Martínez S. & C. H. Ramos 24021* (MEXU, MO).

*Inga calcicola* podría incluirse en la serie *Longiflorae* de Bentham, y se parece a *I. longiflora* Spruce ex Benth. de Brasil, por contar con flores pediceladas, pero no es muy cercana, difiriendo de ella en un gran número de caracteres.

Es interesante anotar, para la interpretación del uso de los caracteres en *Inga*, que la corola de esta especie continua creciendo aún después de la antesis, la cual ocurre al inicio del día; así en la mañana (*Sousa 13048, 13066*) la flor ya abrió y los estambres están erectos, pero la corola no sobrepasa el cáliz, mientras que en la tarde (*Sousa 13090*) la corola ya creció y mide casi el doble del largo del cáliz (sólo en el segundo caso se revisaron las flores mañana y tarde; las primeras colectas ocurrieron en la mañana). Por otro lado cuando en botón, la protocorola es más pequeña que el cáliz.

**Inga calderonii** Standley, J. Wash. Acad. Sci. 13: 352. 1923 (como "calderoni"). TIPO: El Salvador: *Calderón 1392* (holotipo, US; isotipo, GH).

Especie muy interesante la cual en flor se parece mucho a y de hecho ha sido confundida con *Inga vera* Willd., pero se distingue de ésta por las glándulas interfoliolares largamente estipitadas. En fruto sus relaciones se inclinan hacia el grupo de *I. villosissima* Benth. y quizá podría haber tenido su origen en la cruza de *I. vera* e *I. tenella* M. Sousa. Se mantiene como especie válida ya que sus caracteres parecen estables.

*Material representativo.* MEXICO. CHIAPAS: *Sousa et al. 11820* (MEXU). GUATEMALA. ESCUINTLA: *Harmon 1934* (MO). SACATEPEQUEZ: *Roe 786* (WIS). SUCHITEPEQUEZ: *Standley 88950* (F). EL SALVADOR. AHUACHAPAN: *Croat 42101* (MO). LA LIBERTAD: *Calderón 1513* (GH). SONSONATE: *Tucker 1338* (F).

**Inga ciliata** C. Presl, Symb. Bot. 2: 11, t. 58. 1834. TIPO: Brasil: *Lhotky s.n.* (holotipo, PR; isotipo, G).

Para sinónimos véase a Bentham (1876) agregando a *I. leptantha* Benth.

Especie hasta hace poco reportada sólo de la costa este de Brasil, sin embargo han empezado a obtenerse colectas de Ecuador y Perú así como de Mesoamérica en Costa Rica y Panamá, estas últimas reconocidas por Zamora (en prensa).

*Inga ciliata* C. Presl es una especie muy variable en cuanto al número de sus folíolos y sus glándulas interfoliolares largamente estipitadas a sésiles. Este último carácter varía aun en la misma rama (*Martius 1093*, MO), y siendo el carácter que empleó Bentham (1845) para distinguir a *I. ciliata* (elevada) de *I. leptantha* (largamente estipitada), no es posible mantenerlas aparte; además de que la lámina (t. 58) de la descripción original de *I. ciliata* claramente ilustra a las glándulas estipitadas.

Dentro de la variación de *Inga ciliata*, con folíolos un poco más grandes y raquis floral más robustos, dísticos y nudosos, podría entrar muy bien *I. disticha* Benth. de las Guayanas y del norte de Brasil; sin embargo, por el momento las mantenemos separadas.

Con la nueva distribución de *Inga ciliata*, tam-

bién se agrega una serie más para Mesoámerica, la serie *Leptanthae* Benth.

*Material representativo.* COSTA RICA. LIMON: *Mori 348* (WIS). PANAMA. COCLE: *Folsom 3147* (MO). ECUADOR. NAPO: *Neill et al. 7960* (MO). PERU. AMAZONAS: *Huashikat 1446* (MO). BRASIL. (NORDESTE) BAHIA: *Salzmann s.n.* (MO); (SUDESTE) RIO DE JANEIRO: *Luschnath s.n.* (K).

**Inga cocleensis** Pittier, Contr. U.S. Natl. Herb. 18: 211. 1916. TIPO: Panamá: *R. S. Williams 405* (holotipo, NY).

De esta especie Elias (1967) nombró una variedad de flor más grande para Sudamérica, *Inga cocleensis* var. *megantha* T. S. Elias, la cual debe ser una subespecie ya que se trata una variación geográfica.

**Inga cocleensis** subsp. **cocleensis**

*Material representativo.* BELICE. EL CAYO: *Meave & Howe 1420* (MEXU). TOLEDO: *Gentle 5214* (LL). GUATEMALA. IZABAL: *Standley 72586* (F). HONDURAS. ATLANTIDA: *Nelson et al. 3403* (MO). COLON: *Saunders 627* (BM). CORTES: *Molina R. 11799* (NY). NICARAGUA. RIO SAN JUAN: *Moreno 23008* (MO). ZELAYA: *Moreno 24986* (MO). COSTA RICA. HEREDIA: *McDowell 718* (LL). PANAMA. COCLE: *R. S. Williams 405* (NY). COLON: *Gómez-Pompa et al. 3507* (MEXU). PANAMA: *Correa et al. 556* (F). ZONA DEL CANAL: *Croat 7941* (MO).

**Inga cocleensis** subsp. **megantha** (T. S. Elias) M. Sousa, stat. nov. *I. cocleensis* var. *megantha* T. S. Elias, Phytologia 14: 211. 1967. TIPO: Colombia: *Pérez-Arbelaez & Cuatrecasas 6458* (holotipo, US).

*Material representativo.* COLOMBIA. CHOCO: *Gentry & Libenson 30366* (MO). VALLE: *Mazuera 30* (MO). VENEZUELA. ZULIA: *Davidse et al. 18297* (MO).

**Inga cookii** Pittier, Contr. U.S. Natl. Herb. 18: 203. 1916. TIPO: Guatemala: *Cook & Griggs 505* (holotipo, US).

*Inga subvestita* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 27. 1940. TIPO: Guatemala: *C. L. Wilson 315* (holotipo, F).

Especie cuya legumbre no se conocia hasta su colecta (*Contreras 10337*) en 1970, la cual tiene dimensiones de 4–7.5 × 1.8–2.5 × 0.3 cm, es aplanada, oblonga, derecha, sésil, apiculada y tomentosa con tricomas pardo-amarillentos. Sin embargo, se le han adjudicado frutos de otras especies: así primero Standley y Steyermark (1946) le asignan el fruto de *Inga pavoniana* Don, tanto por su descripción, nombre vulgar de "machetón," localidad y colecta (véase *Standley 92857*, F). Después León (1966) sí cita dos colecciones de Honduras (*Yuncker et al. 6292, 6678*), tratandose de *I. tenella* M. Sousa. En el caso de León (1966) es interesante comentar que en efecto existen ejemplares (como *Molina R. 24244*, NY; *25431*, BM) que en gran medida son intermedios entre *I. cookii* e *I. tenella*.

*Material representativo.* GUATEMALA. ALTA VERAPAZ: *Steyermark 45159a* (F). EL PETEN: *Lundell & Contreras 20655* (MO). IZABAL: *Contreras 10337* (LL). HONDURAS. ATLANTIDA: *Standley 54256* (A).

**Inga cordistipula** C. Martius, Flora 20(2): Beibl. 111. 1837. *Mimosa plana* Vell. Conc., Fl. Flumin. 11: t. 10, non 28. 1831. TIPO: Brasil: *Vellozo, Fl. Flumin. 11: t. 10. 1831.*

*Inga urceolata* Zamora, Brenesia 33: 117. 1991. TIPO: Panamá: *McPherson 10496* (holotipo, MO; isotipos, BM, CR, MEXU, US).

Martius (1837) transfiere de género y crea un nuevo nombre específico para *Mimosa plana* Vell. Conc., lámina 10, ésto debido a que la lámina 28 de Vellozo corresponde a una especie de *Acacia* que lleva el mismo nombre.

*Inga cordistipula* es una especie hasta ahora conocida sólo del sureste de Brasil. En Panamá, su variación es reducida, pero en Brasil varía grandemente, estando representados todos los caracteres que la podrían distinguir en Mesoamérica; así su raquis foliar terete, está ilustrado por Barroso (1965) para Guanabara [=Rio de Janeiro] y los folíolos más anchos, se aprecian en el sinónimo *I. fluvii-novi* Harms (*Schwacke 8811*, B, foto MO). Sin embargo, el material de Panamá tiende a contar con estípulas un poco más angostas, pero tan largas (véase *de Nevers et al. 7382*, MO) como su análogo de Brasil.

*Material representativo.* PANAMA. COLON: *McPherson 8451* (MO). PANAMA: *Nee et al. 8787* (MO). SAN BLAS: *de Nevers et al. 7382* (MO). BRASIL. (SUDESTE) MINAS GERAIS: *Schwacke 8811* (B, foto MO). RIO DE JANEIRO: *Glaziou 2977* (BR).

**Inga coruscans** Humb. et Bonpl. ex Willd., Sp. Pl. ed. 4, 2: 1017. 1806. TIPO: Colombia: *Bonpland 1574* (holotipo, B-W, foto MO).

*Inga caldasiana* Britton et Killip, Ann. New York Acad. Sci. 35: 115. 1936. TIPO: Colombia: *Mutis 3539* (holotipo, US).

Esta especie se caracteriza, dentro de la sección *Bourgonia* Benth., por contar con folíolos relativamente grandes y hojas brevipecioladas.

*Inga coruscans* es de amplia distribución, pero

muy mal colectada o quizá de distribución esporádica, tanto en Mesoamérica como en Sudamérica.

*Material representativo.* COSTA RICA. CARTAGO: *Tonduz 12991* (BM). PUNTARENAS: *Liesner 1829* (MO). PANAMA. CHIRIQUI: *Croat 22161* (WIS). DARIEN: *Duke 13004* (NY). COLOMBIA. ANTIOQUIA: *Soejarto et al. 4136* (A). BOYACA: *Lawrance 784* (MO). GUYANA: *de la Cruz 3599* (MO). ECUADOR. LOS RIOS: *Dodson 5227* (MO). PERU. LORETO: *Encarnación E-1087* (MO). PASCO: *Smith 3928* (MO). BOLIVIA. COCHABAMBA: *Steinbach 448* (MO). BRASIL. (NORTE) AMAZONIA: *Krukoff 4769* (K).

**Inga cuspidata** M. Sousa, sp. nov. TIPO: Panamá. Bocas del Toro: Río San Pedro, Jan. 1978, *B. L. Gordon 3* (holotipo, MO).

Specie *Ingae multijugae* Bentham propinqua, ab ea tamen foliolis ex anguste lanceolatis ellipticis, apice cuspidato, inflorescentiis paucifloris, rhachide florifera brevi, necnon legumine angustiore valvis strigulosis praedito satis diversa.

Arboles 10–12 m; ramas teretes, ferrugíneo tomentulosas cuando jóvenes, posteriormente glabrescentes. Hojas 12–18-folioladas; estípulas 4–6 mm, liguladas, triangulares a filiformes, más o menos persistentes; pecíolo 0.7–2.5 cm, terete; folíolos tenuemente discoloros, cartáceos, la base cuneada, el ápice cuspidado, el haz opaco, glabro excepto tomentoso sobre la nervadura primaria, el envés rojizo, esparcidamente seríceo con tricomas canescentes a pardo-amarillentos, la nervadura primaria eglandular; par basal de folíolos 3–4 × 0.9–1.6 cm, lanceolados a elípticos, el par apical 10.5–12.5 × 2.6–3.6 cm, lanceolados a angostamente elípticos; raquis foliar 8.5–20 cm, generalmente terete, rara vez angostamente alado, el ala hasta 4 mm ancho, oblanceolada; glándulas interfoliolares casi sésiles a brevistipitadas, el estípite robusto, cupuliformes, el cuerpo glandular 1.8–2 × 1.8–2 mm; apéndice 3–4 mm, filiforme. Inflorescencias en espigas solitarias; pedúnculo 4–6 cm, terete, inconspicuamente estriado, tomentoso a velutino con tricomas ferrugíneos; raquis floral 1–2 cm, paucifloro, las flores congestas, las brácteas aparentemente homomorfas ca. 2 mm, cuculadas, pronto caducas. Flores sésiles; botones florales con el cáliz abierto, apiculados; cáliz 11–15 mm, tubular, estriado, seríceo con tricomas pardo-amarillentos, con escotaduras, los lóbulos 2.5–3 mm, triangulares; corola 25–29 mm, tubular a subturbinada, amarillenta, vellosa con tricomas pardo-amarillentos; tubo estaminal inserto. Legumbre 10–17.5 × 1.5–2.1 × 0.8–1.1 cm, algo aplanada a más bien túrgida, derecha a curveada, linear-oblonga, sésil o casi sésil, apiculada en el ápice, estrigulosa (más densamente sobre las suturas), las valvas inconspicuamente nervadas, las suturas derechas, multisulcadas, los márgenes de las suturas redondeados.

*Distribución y hábitat.* Endémica de la vertiente Caribe de Panamá, en las provincias de Bocas del Toro y San Blas. Esta especie habita bajo condiciones riparias y de vegetación secundaria, en altitudes hasta de 200 m. Florece en diciembre y enero y fructifica a partir de enero a abril.

*Nombres vernáculos.* Guamo de monte, bungguagua (en Guaymí).

*Usos.* Los Kuna usan la pulpa dulce alrededor de las semillas como comestible.

*Paratipos.* PANAMA. BOCAS DEL TORO: Río San Pedro, *B. L. Gordon 41* (MO). SAN BLAS: Río Cartí Grande, 9°21′N, 79°03′W, *G. de Nevers & H. Herrera 4146* (MO); Río Congandi from village of Congandi to just above its confluence with Río Titamibe, 9°27′N, 79°8′W, *de Nevers et al. 4644* (MO); El Llano–Cartí road, km 26.5, along Río Cartí Chico, 9°19′N, 78°55′W, *de Nevers et al. 5336* (MO); along the Río Sidro at base of Cerro Habú, 9°23′N, 78°49′W, *K. Sytsma et al. 2613* (MO).

*Inga cuspidata* está emparentada con *I. multijuga* Benth., de la cual difiere por varios caracteres (véase diagnosis), además de que en ocasiones los raquis foliares de *I. cuspidata* son alados y el fruto (maduro) es cilíndrico en vez de aplanado. El epíteto hace énfasis en el ápice cuspidado de los folíolos.

**Inga chiapensis** Miranda ex M. Sousa, sp. nov. TIPO: México. Chiapas: en cañada hacia El Aguacate, al N de La Chacona [NO de Tuxtla Gutiérrez], 800 m, en selva alta subdecidua, 19 mar. 1950, *F. Miranda G. 6127* (holotipo, MEXU).

Arbores e mediano procerae, ramis juvenilibus brunneo lutescenti-tomentosis. Folia 2–4-jugata; stipulae 3–4 mm longae, ex ovatae triangulares, deciduae; foliola tenuiter discoloria, chartacea; rhachis foliaris late alata, glandulis ex sessilibus breviter stipitatis, urceolatis. Inflorescentiae spiciformes; rachis floralis 2.5–4 cm longa; bracteae homomorphae cochleatae, deciduae. Flores sessiles; alabastra floralia calyce aperto; calyx tubulosus, striatus, pilosus, emarginatus; corolla tubuloso-subturbinata, brunneo-lutescenti-villosa. Legumen breve, latum, incrassatum, complanatum, brunneo-lutescenti-hirsutum.

Arboles 5–18 m; ramas teretes, tomentosas con tricomas pardo-amarillentos cuando jóvenes, posteriormente glabrescentes. Hojas 4–8-folioladas; estípulas 3–4 mm, ovadas a triangulares, caducas; pecíolo 1–3.5 cm, terete a alado; folíolos ligeramente discoloros, cartáceos, la base ligeramente asimétrica, cuneada a obtusa, el ápice acuminado a cuspidado, el haz ligeramente brillante, piloso después glabrescente, el envés opaco, esparcida-

mente tomentoso, las nervaduras tomentosas con tricomas pardo-amarillentos; la nervadura primaria eglandular; par basal de folíolos 3.7–7 × 2.2–3.5 cm, generalmente elípticos en ocasiones ovados, el par apical 9.5–16 × 4–7.5 cm, lanceolados a elíptico-lanceolados; raquis foliar (2.8–)3.5–9(–15) cm, alado, el ala hasta 16 mm de ancho, oblanceolada, raramente obtriangular; glándulas interfoliolares sésiles a brevistipitadas, urceoladas, el cuerpo glandular 0.6–0.7 × 0.6–0.7 mm; apéndice 9–11 mm, setiforme, pronto caduco. Inflorescencias en espigas, generalmente solitarias; pedúnculo (1.5–)3–6.5 cm, subterete, inconspicuamente sulcado, tomentoso con tricomas pardo-amarillentos; raquis floral 2.5–4 cm, las flores esparcidas proximalmente, congestas distalmente, las brácteas homomorfas 1.3–1.8 mm, cóncavas, oblanceolado-cocleadas a ovado-cocleadas, caducas, las bases cortamente decurrentes. Flores sésiles; botones florales con el cáliz abierto, obtusos; cáliz 8–10 mm, tubular, estriado, piloso, con escotaduras, los lóbulos 1.5–2 mm, triangulares; corola 15–18 mm, tubular-subturbinada, verdosa, moderadamente vellosa con tricomas pardo-amarillentos; tubo estaminal inserto, blanco. Legumbre 8–12.5 × 3.2–3.6 × 1.5–2 cm, aplanada, derecha, oblonga, sésil en la base, apiculada a obtusa en el ápice, hirsuta con tricomas pardo-amarillentos, las valvas aplanadas, las suturas derechas, redondeadas, los márgenes de las suturas 1-sulcados.

*Distribución y hábitat.* Conocida solamente de dos áreas bien definidas, el margen norte de la Depresión Central de Chiapas en vegetación de selvas bajas a altas subcaducifolias a caducifolias y en la zona de Uxpanapa, Veracruz, en selvas altas perennifolias con *Dialium*, *Ormosia* (Leguminosae), *Terminalia* (Combretaceae), *Licania* (Chrysobalanaceae), *Calophyllum*, *Symphonia* (Guttiferae), *Guarea* (Meliaceae), *Sloanea* (Elaeocarpaceae), *Sterculia* (Sterculiaceae), y *Tapirira* (Anacardiaceae). En altitudes de 200 m y de 850–1,100 m. Florece de mediados de marzo a principios de mayo; fructifica de junio a septiembre.

*Paratipos.* MEXICO. VERACRUZ: Mpio. Jesús Carranza, lomas al S de Poblado 2 (±3 6 km al S del entronque de terracería La Laguna–Sarabia con camino a Ejido La Paz), 17°12′N, 94°38′30″O, *T. Wendt et al. 5304, 5633* (CHAPA, MEXU). CHIAPAS: Mpio. Ocozocoautla, a 1 km al NO del entronque Aeropuerto–Ocozocoautla–México, carretera 190, *A. Reyes G. 555* (MEXU, MO); Mpio. San Fernando, San Fernando, *F. Miranda G. 7219* (MEXU); Mpio. Tuxtla Gutiérrez Cerro Hueco, al SSE de Tuxtla Gutiérrez, *Miranda 5570, 6878* (MEXU); en cañada hacia El Aguacate, cerca y al N de La Chacona, *Miranda 6413* (MEXU); adelante Mirador La Coyota, El Sumidero, *Miranda 7662, 7718* (MEXU); entre los km 18–22 de la carretera de Tuxtla Gutiérez hacia el Cañon del Sumidero, *O. Téllez V. et al. 6690, 7578* (MEXU).

*Inga chiapensis* muestra en Mesoamérica similitudes con *I. mucuna* Walp. et Duchass. e *I. leonis* Zamora; con esta última son más estrechas, pero no suficientes para unirlas. Su variación se puede agrupar en la de la Depresión Central de Chiapas y la de Uxpanapa, Veracruz: en la primera área *I. chiapensis* muestra el cáliz ligeramente mayor, la corola más chica y las hojas que tienden a poseer más folíolos que en el área de Uxpanapa, además que varían en cuanto a hábitats y altitud. Sin embargo, por el momento las mantengo bajo un sólo epíteto con la posible distinción posterior en categorías infraespecíficas, dependiendo de más colectas, sobre todo del área baja húmeda de Uxpanapa. Esta especie fue reconocida como entidad nueva por Faustino Miranda González hace más de 40 años y en su honor se emplea el epíteto que él designó, a pesar de que ya se le conoce hoy en día fuera de Chiapas.

**Inga chocoensis** Killip ex T. S. Elias, Phytologia 14: 210. 1967. TIPO: Colombia: *Cuatrecasas 16372* (isotipo, F).

*Inga coprocarpa* Zamora et Poveda, Brenesia 33: 101. 1991. TIPO: Costa Rica: *Herrera & Rivera 842* (holotipo, CR; isotipos, MEXU, MO).

Esta interesante especie está cercanamente emparentada con *Inga longipes* Benth. del alto Amazonas de Perú e *I. duquei* Harms del Valle de Cauca en Colombia; sin embargo, hay varios caracteres que las separan.

*Material representativo.* NICARAGUA. MATAGALPA: *Neill 1746* (MO). COSTA RICA. ALAJUELA: *Utley & Utley 3213* (F). HEREDIA: *Bawa 544* (MO). PANAMA. BOCAS DEL TORO: *Proctor Cooper 527* (F). COCLE: *Croat 67470* (MO). PANAMA: *Porter et al. 4185* (MO). COLOMBIA. VALLE: *Cuatrecasas 16098* (F). ECUADOR: ESMERALDAS: *Little & Dixon 21023* (MO).

**Inga dasycarpa** M. Sousa, sp. nov. TIPO: México. Chiapas: 12 km al E de Tziscao, sobre el camino a Santa Elena, en el Parque Nacional Lagos de Monte Bello, 1 oct. 1983, *E. Cabrera & H. de Cabrera 5885* (holotipo, MEXU; isotipo, MO). Figura 2.

Arbores medianae; rami juveniles dense ferrugineo-tomentosi. Folia 2–3-jugata; stipulae 1.5–2 mm longae, ligulatae; foliola ex chartacea coriacea; rhachis foliaris alata glandulalis ex subsessilibus stipitatis praedita. Inflorescentiae capituliformes; pedunculus 1 1.3 cm longus; rhachis floralis subglobosa; bracteae ligulatae. Flores sessiles; calyx 7–9 mm longus, tubularis, inconspicue stria-

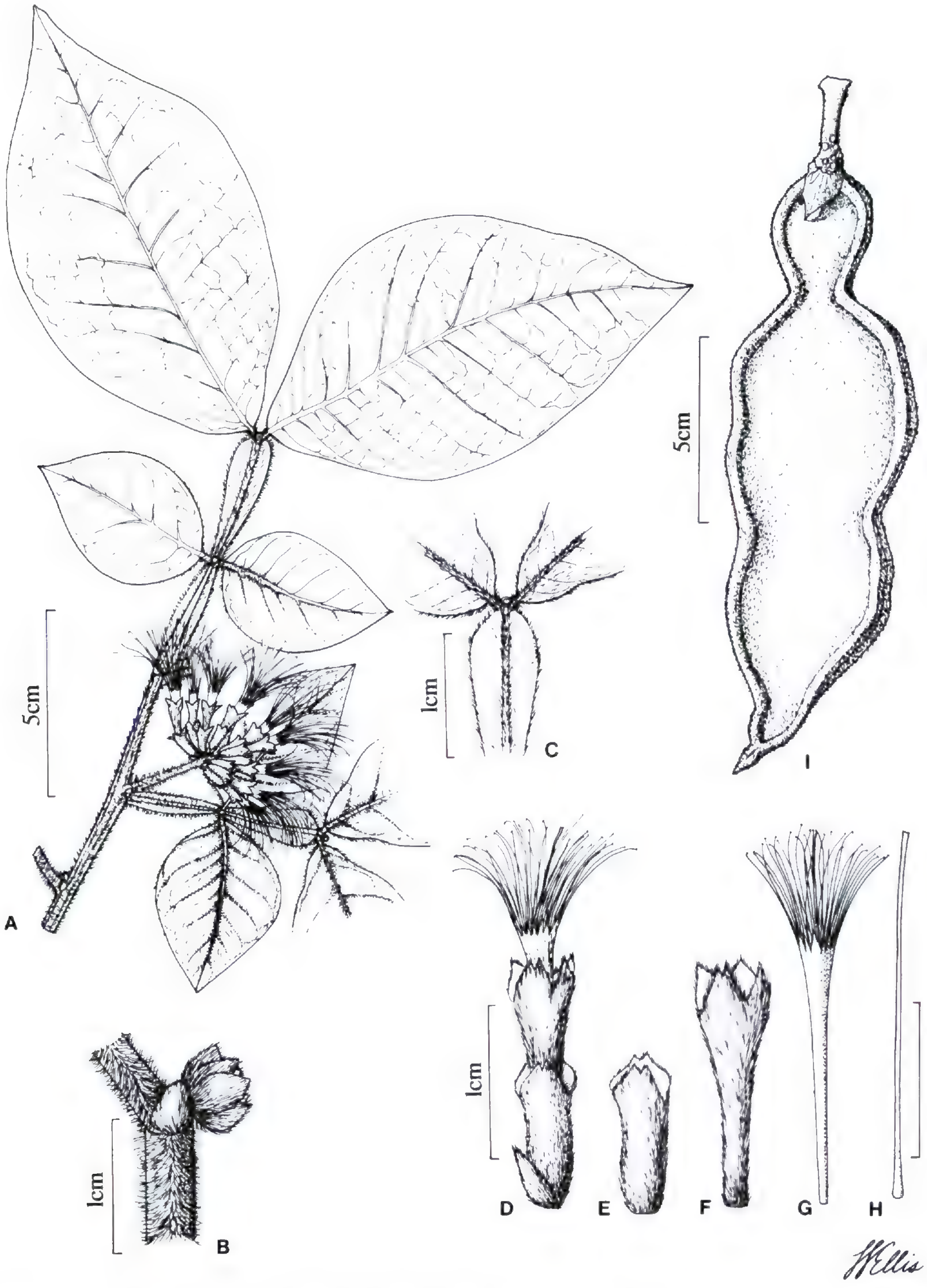


FIGURA 2. *Inga dasycarpa* M. Sousa.—A. Rama con inflorescencia.—B. Detalle de estípulas.—C. Glándula interfoliolar.—D. Flor.—E. Cáliz.—F. Corola.—G. Tubo estaminal. -H. Gineceo. (Tomado de *E. Cabrera 5885.*)—I. Fruto. (Tomado de *O. Téllez 642.*)

tus; corolla 17–19 mm longa. Legumen usque ad 6.5 cm latum, complanatum, oblongum, ferrugineo-hirsutum.

Arboles 4–15 m; ramas teretes, densamente ferrugíneo tomentosas cuando jóvenes, posteriormente glabrescentes. Hojas 4–6 folioladas; estípulas 1.5–2 mm, liguladas, caducas; pecíolo 1–2 cm, terete a alado; folíolos generalmente concoloros, en ocasiones ligeramente discoloros, cartá-

ceos a coriáceos, la base simétrica a ligeramente asimétrica, obtusa a cuneada, el ápice agudo a acuminado, el haz ligeramente brillante, moderadamente a esparcidamente piloso, el envés opaco, moderadamente piloso, la nervadura primaria eglandular; par basal de folíolos 3.3–5.1(–7) × 1.1–2.5(–4.5) cm, ovados a lanceolados, el par apical 7–10(–12.5) × 3.2–5.2(–7) cm, elípticos a obovados; raquis foliar 2.5–4(–7) cm, alado, el ala 5–7(–13) mm de ancho, elíptica, generalmente oblanceolada, rara vez obtriangular; glándulas interfoliolares subsésiles a estipitadas, clavuliformes, el cuerpo glandular 0.7–0.9 × 0.7–0.9 mm; apéndice, ausente. Inflorescencias capituliformes, 1–2 fasciculadas; pedúnculo 1.1–3 cm, subterete, inconspicuamente sulcado, ferrugíneo tomentoso; raquis floral ca. 4 mm, subgloboso, las flores congestas, las brácteas homomorfas 1.5–2 mm, cóncavas, liguladas, caducas. Flores sésiles; botones florales con el cáliz cubriendo, desconocidos; cáliz 7–9 mm, tubular, inconspicuamente estriado, tomentoso con tricomas pardo-amarillentos, con escotaduras, los lóbulos 1.5–2 mm, ligulados; corola 17–19 mm, infundibuliforme, blanca, canescente vellosa; tubo estaminal inserto, blanco. Legumbre 15–21 × 4–6.5 × 0.8–1.5 cm, aplanada, derecha, oblonga, sésil, apiculada a rostrada en el ápice, ferrugíneo hirsuta, las valvas aplanadas, las suturas más o menos derechas, marginadas, los márgenes de las suturas 1-sulcados.

*Distribución y hábitat.* De Chiapas, México a Cortés, Honduras en regiones montañosas, en vegetación de bosques caducifolios con *Liquidambar* (Hamamelidaceae), *Magnolia* (Magnoliaceae), *Clethra* (Clethraceae), *Vochysia* (Vochysiaceae), también en bosques de *Pinus* y *Quercus*. En altitudes entre los 1,350 a 1,600 m. Florece en octubre y fructifica de diciembre a abril.

*Paratipos.* MEXICO. CHIAPAS: Mpio. La Trinitaria, 15 km E of La Trinitaria on road to Montebello, *D. E. Breedlove 42062* (MEXU, MO); E of Laguna Tziscao, Monte Bello National Park, *M. Sousa et al. 11876* (BM, MEXU, MO); a 10 km al E de Montebello, a 1 km de la Laguna de Tziscao, *O. Téllez V. et al. 642* (MEXU). HONDURAS. CORTES: Montaña San Idalfonso entre Bañaderos y Cusuco, *A. Molina R. 11459* (LL, NY, US).

*Inga dasycarpa* se encuentra muy relacionada con *I. villosissima* Benth. de las montañas de Venezuela, pero en *I. dasycarpa* las inflorescencias tienden a ser capituliformes, las brácteas más pequeñas y pronto caducas, las flores más chicas y las estípulas de menor tamaño y pronto deciduas. También está muy relacionada con *I. tenella* M. Sousa, difiriendo de ella por tener *Inga dasycarpa* inflorescencias capituliformes, flores y legumbres de mayor talla, y las hojas coriáceas que en general poseen menos folíolos. *Inga dasycarpa* e *I. tenella* son dos especies que en gran medida son simpátricas, tanto en áreas geográficas generales como en los mismos hábitats, sin que hayamos encontrado posibles híbridos. Estas especies aparentemente refuerzan su aislamiento con períodos de floración diferentes. El epíteto hace referencia a la pelosidad de la legumbre.

**Inga davidsei** M. Sousa, sp. nov. TIPO: Guatemala. Izabal: El Estor, 23 Mar. 1972, *E. Contreras 11483* (holotipo, MEXU; isotipos, LL, MO). Figura 3.

Species *Ingae goldmanii* Pittier proxima, a qua tamen foliis foliola numerosiora habentibus, stipulis longioribus quam latioribus, foliolis coriaceis et supra nitentibus, glandulis per nervum medium absentibus, appendice rhachidea praesente, glandulis interfoliolaribus longe stipitatis, floribusque maioribus recedit.

Arboles 7–20 m; ramas subteretes, ferrugíneo hirsútulas cuando jóvenes, posteriormente glabrescentes. Hojas (6–)8(–10)-folioladas; estípulas (5–)7–14 mm, liguladas a triangulares, caducas; pecíolo (1.5–)2.5–5 cm, terete; folíolos discoloros subcoriáceos, la base simétrica a casi simétrica, cuneada, el ápice obtuso a acuminado, el haz brillante, glabro excepto ferrugíneo tomentoso en la nervadura primaria, el envés opaco, piloso con la nervadura primaria tomentosa como el haz, la nervadura primaria eglandular; par basal de folíolos 7–9.5(–13) × 3.2–4.3(–9) cm, elípticos a oblongo-elípticos, el par apical 15–18(–23) × 5.5–9 (–11.5) cm, generalmente elípticos, en ocasiones obovados; raquis foliar 9.5–15 cm, ferrugíneo tomentoso, terete, marginado a angostamente alado principalmente entre los 3 pares distales de folíolos, el ala hasta 9 mm de ancho, elíptica; glándulas interfoliolares generalmente largamente estipitadas, clavuliformes, el cuerpo glandular 0.5–0.9 × 0.5–0.9 mm; apéndice 10–25 mm, setiforme, arqueado, caduco. Inflorescencias en espigas solitarias; pedúnculo 6–8.5 cm, terete, aparentemente liso, ferrugíneo tomentoso; raquis floral 0.6–1 cm, las flores congestas, las brácteas homomorfas 6–9 mm, gruesas, ligeramente concavas triangular-liguladas, una estéril en el ⅓–½ superior del pedúnculo, persistentes. Flores sésiles; botones florales con el cáliz cubriendo desconocidos; cáliz 17–19 mm, ciatiforme, lanoso con tricomas pardo a pardo-amarillentos, sin escotaduras, los lóbulos 3–4 mm, triangular-ligulados; corola 28–32 mm, subturbinada, pardo-amarillento lanosa; tubo estaminal inserto, blanco. Legumbre 24–30 × 3.3–6.5

FIGURA 3. *Inga davidsei* M. Sousa.—A. Rama con inflorescencia.—B. Detalle de estípulas.—C. Glándula interfoliolar.—D. Flor.—E. Cáliz.—F. Tubo estaminal.—G. Gineceo. (Tomado de *E. Contreras 11483.*)—H. Fruto. (Tomado de *G. Davidse & A. Brant 32330.*)

× 0.9–1.5 cm, aplanda, ligeramente espiralada, oblonga sésil en la base, apiculada en el ápice, ferrugíneo hirsuta, las valvas aplanadas, las suturas derechas, redondeadas, los márgenes de las suturas aplanados a 1-sulcados.

*Distribución y hábitat.* Al sur de la Península de Yucatán, en el norte de Guatemala, Belice, y Honduras en selvas bajas a medianas caducifolias, en sitios riparios y en la orilla de un pinar, sobre suelos someros arcillosos, en altitudes entre los 100

a 900 m. Florece de mediados de febrero a marzo y fructifica de marzo a abril.

*Nombres vernáculos.* Palo de paterno silvestre, cola de mico.

*Usos.* El fruto es comestible y tiene sabor a frijoles.

*Paratipos.* BELICE. EL CAYO: Dent's Drive, Augustine Mountain Pine Ridge *D. R. Hunt 484* (BM, LL, US). TOLEDO: lower part of Richardson Creek, affluent of Bladen Branch, lower part of Maya Mountains, 16°33′N, 88°46′–48′W, *G. Davidse & A. E. Brant 32330* (MEXU, MO). GUATEMALA. ALTA VERAPAZ: *Cook & Griggs 380* (US). HUEHUETENANGO: Cerro Jolomtac, above Finca San Rafael, Sierra de los Cuchumatanes, *J. A. Steyermark 49146* (A, F, US). IZABAL: Lago de Izabal, Mariscos, *T. D. Pennington & D. MacQueen 13437* (K). HONDURAS. ATLANTIDA: Lancetilla, Miramar -San Isidro, *R. Cruz 275* (TEFH); Las Mangas road La Ceiba–Yaruca, above Las Mangas, *Pennington & P. House 13404* (K).

*Inga davidsei* está emparentada con *I. goldmanii* Pittier del sur de Mesoamérica al norte de Sudamérica; sin embargo, difiere de ella tanto en caracteres vegetativos como en cuanto al tamaño de la flor (véase diagnosis).

Se dedica esta especie al Gerrit Davidse (1942–), botánico distinguido de Jardín Botánico de Missouri y colega del autor en el proyecto *Flora Mesoamericana*, quien colectó esta especie bajo el desarrollo del proyecto.

**Inga densiflora** Benth., Trans. Linn. Soc. London 30: 617. 1875. TIPO: Perú. San Martín: Tarapoto, *Spruce 4504* (fl, fr) (lectotipo, designado aquí, K herb. Benth.; isolectotipos, GH, K (3 ej.)).

Para sinónimos véase León (1966).

León (1966) designó a *Spruce 4504* como el tipo de *Inga densiflora* sin mencionar el herbario en que está depositado ni qué ejemplar, por lo que se considera una lectotipificación incompleta. Aquí se lectotipifica designando a K en el herb. Bentham, al ejemplar con flores y frutos.

*Inga densiflora* Benth., como ya lo apuntó León (1966), es una especie muy variable, particularmente en la pelosidad y en la forma de sus glándulas interfoliolares. También a esta variación, seguramente, el hombre ha contribuido, así como a ampliar su distribución, por su uso como sombra de café. Es muy probable que en el área cafetalera del Soconusco en Chiapas, México, el hombre sea el responsable de la presencia de esta especie, aunque en la actualidad se encuentra también en estado silvestre "escapada."

*Material representativo.* MEXICO. CHIAPAS: *Martínez S. 19847* (MEXU). GUATEMALA. RETALHULEU: *MacQueen & Hughes 14* (MEXU). NICARAGUA. CHONTALES: *Bunting & Licht 1173* (F). MATAGALPA: *J. B. Salas & B. W. Taylor 2485* (EAP). ZELAYA: *Sandino 3447* (MO). COSTA RICA. ALAJUELA: *Croat 46799* (MO). CARTAGO: *Córdoba 388* (MO). GUANACASTE: *Sousa et al. 12735* (MEXU). HEREDIA: *Bawa 599* (MO). PUNTARENAS: *Koptur 77* (MO). SAN JOSE: *Montealegre 1* (CR). PANAMA. COCLE: *R. S. Williams 316* (US). CHIRIQUI: *Croat 33159* (MO). HERRERA: *McPherson 10285* (MO). SAN BLAS: *Cooper 651* (NY). VERAGUAS: *Gentry 6232* (MO). COLOMBIA. ANTIOQUIA: *Archer 658* (US). CAUCA: *Lehmann 904* (US). VALLE: *Langlassé 63* (US). VENEZUELA. DISTRITO FEDERAL: *Pittier 13028* (MO). TACHIRA: *Steyermark et al. 119675* (MO). YARACUY: *Davidse et al. 20916* (MO). ECUADOR. NAPO: *Cerón & Cerón 3056* (MO). PERU. MADRE DE DIOS: *Young & Stratton 234* (MO). SAN MARTIN: *Spruce 4504* (GH).

**Inga dwyeri** M. Sousa, sp. nov. TIPO: Panamá. Panamá: Cerro Jefe to 2,900 ft., 5 Jan. 1972, *J. D. Dwyer & A. Gentry 9494* (holotipo, MO; isotipo, MEXU).

Arbores parvae ramis juvenilibus ferrugineo-hirsutulum. Folia (2–)3-jugata; stipulae 2–3.5(–5) mm longae, persistentes; foliola chartacea bullata; rhachis foliaris teres, interdum anguste alata, glandulis ex subsessilibus stipitatis, claviformibus ornata. Inflorescentiae spicatae, angustae; rhachis floralis brevis, floribus distantibus, bracteis concavis, ovatis, persistentibus (in fructificacatione interdum lignescentibus). Flores sessiles; alabastra floralia calyce clauso, attenuato; calyx tubulosus, striatus, sparse ferrugineo-villosus, emarginatus, corolla tubulosa, canescenti luteo-villosa. Legumen parvum, complanatum, oblongum, brunneo-luteo-hirsutum.

Arboles 3–10 m; ramas teretes, ferrugíneo hirsútulas cuando jóvenes, posteriormente glabrescentes. Hojas (4–)6-folioladas; estípulas 2–3.5(–5) mm, ovado-cordatas a triangular-subuladas, persistentes; pecíolo 1–1.8(–3) cm, terete a marginado; folíolos ligeramente discoloros, cartáceos, abollados, la base asimétrica a ligeramente asimétrica, cuneada a truncada, el ápice mucronulato a acuminado, el haz opaco, casi glabro excepto ferrugíneo tomentoso en la nervadura primaria, el envés opaco con pelosidad similar al haz, la nervadura primaria eglandular; par basal de folíolos 3.2–7(–11) × 2.1–3.7(–4.8) cm, ovados a elípticos, el par apical 7–9 × 2.8–4.2 cm, elípticos a subobovados; raquis foliar 1.5–4.1(–7.5) cm, generalmente terete, en ocasiones alado, el ala hasta 4 mm de ancho, angostamente oblanceolada; glándulas interfoliolares subsésiles a robustamente estipitadas, claviformes, el cuerpo glandular 0.6–0.8 × 0.6 0.8 mm; apéndice 2–3 mm, pronto caduco. Inflorescencias en espigas, 1–3 fasciculadas; pedúnculo (0.5–)2.5–4.5 cm, delgado, más o menos aplanado, sulcado, ferrugíneo hirsútulo; raquis floral 1.3–3 cm, las flores espaciadas, las brácteas homomorfas, 2–3 mm, cóncavas, ovadas,

persistentes (en fruto en ocasiones lignifican). Flores sésiles; botones florales con el cáliz cerrado, atenuado-apiculado; cáliz 6–9 mm, tubular, estriado, esparcidamente ferrugíneo velloso, con escotaduras, los lóbulos 1.2–1.8 mm, triangulares; corola 13–17 mm, tubular, vellosa con tricomas canescentes a amarillos; tubo estaminal exerto, blanco. Legumbre 9–10.5 × (1.9–)2.6–2.9 × 0.3–0.7 cm, aplanada, derecha, oblonga, sésil, apiculada a rostrada en el ápice, moderadamente hirsuta con tricomas pardo-amarillentos, las suturas derechas a constrictas, nervadas, los márgenes de las suturas aplanados a sulcados.

*Distribución y hábitat.* Sólo conocida de Panamá, entre 225 y 950 m. Florece en febrero, abril, y septiembre y fructifica de noviembre a enero.

*Paratipos.* PANAMA. DARIEN: Rio Pierre, 10 mi. S of El Real near Dos Bocas, *R. Foster & T. Lowenbach 2272* (MO). PANAMA: Goofy Lake to ca. 8 mi. S of Goofy Lake toward Cerro Jefe, *J. D. Dwyer 7069A* (MO); Cerro Azul, *A. Gentry 6132* (F, MO); along El Llano to Cartí road, about 8 mi. from Pan-American highway, *G. McPherson 10487* (MO). SAN BLAS: El Llano–Cartí Road, 9°19′N, 78°55′W, *H. Herrera & S. Kaza 7334* (MO).

Especie muy variable, cuyas hojas de brotes vegetativos además de ser de mayor talla, tienden a tener el raquis foliar alado. Muy característica por sus folíolos abollados y sus inflorescencias esbeltas y laxas con brácteas persistentes. Sus relaciones en Mesoamérica parecen ser con *Inga pinetorum* Pittier e *I. hayesii* Benth.

Se dedica esta especie a John D. Dwyer (1915–), quien ha contribuido grandemente al conocimiento de la florística mesoamericana.

**Inga edulis** C. Martius, Flora 20: Beibl. 113. 1837. *Mimosa ynga* Vell. Conc., Fl. Flumin. 11: t. 3. 1831, non L. TIPO: Brasil: *Vellozo, Fl. Flumin. 11: t. 3. 1831.*

Especie muy característica por su robustez tanto de hojas y flores como de fruto. Bajo este concepto *Inga edulis* no se le ha colectado o es escasa en las Guayanas, donde *I. scabriuscula* Benth. habita.

*Inga edulis* es sin duda una especie de la Amazonia, que como propone León (1966) posiblemente fue introducida por el hombre a Mesoamérica y quizá también en Colombia: Antioquia y Chocó, ya que siempre está asociada con asentamientos humanos y en plantaciones de café y cacao.

*Material representativo.* HONDURAS. MORAZAN: *Standley 16086* (F). NICARAGUA. ZELAYA: *Bunting & Licht 679* (F). COSTA RICA. LIMON: *Grayum & Sleeper 4357* (MO). PANAMA. BOCAS DEL TORO: *Todzia 2560* (TEX). CHIRIQUI: *Schmalzel 1332* (MO). DARIEN: *Croat 27311* (MO). PANAMA: *Gentry 2145* (MO). COLOMBIA. AMAZONAS: *Gillett 16511* (MO). ANTIOQUIA: *Shepherd s.n.* (MO). CAQUETA: *Davidse et al. 563* (MO). CHOCO: *Forero et al. 3070* (MO). VAUPES: *Schultes et al. 24042* (MO). VENEZUELA. AMAZONAS: *Ll. Williams 14452* (MO). DELTA AMACURO: *Marcano Berti 382* (F). ECUADOR. NAPO: *Neill 6318* (MO). PASTAZA: *Neill & Palacios 6558* (MO). PERU. AMAZONAS: *Huashikat 1612* (MO). LORETO: *Croat 17522* (MO). PASCO: *D. N. Smith 3818* (MO). SAN MARTIN: *Knapp et al. 7270* (MO). UCAYALI: *Gentry & Díaz 58361* (MO). BOLIVIA. BENI: *Boom 4563* (NY). BRASIL. (NORTE) AMAZONIA: *Prance et al. 10793* (MO). PARA: *Austin & Cavalcante 4139* (MO).

**Inga exalata** T. S. Elias, Phytologia 14: 208. 1967. TIPO: Costa Rica: *Brenes 3634* (holotipo, F; isotipo, NY).

Esta especie sólo hasta hace poco se colectó en Panamá. Sus relaciones no son muy claras, sin embargo se le puede colocar tentativamente en el complejo de *Inga villosissima* Benth., tanto por su pelosidad general y glándulas interfoliolares como por su legumbre.

*Material representativo.* COSTA RICA. ALAJUELA: *Brenes 17057* (F). CARTAGO: *Poveda 941* (F). PANAMA. COCLE: *McPherson 13632* (MO). PANAMA: *McPherson 12347* (MO).

**Inga filiformis** Zamora, Brenesia 33: 103. 1991. TIPO: Panamá: *Mori et al. 6824* (holotipo, MO; isotipo; CR).

Esta especie tan característica se relaciona, al menos en parte, con *Inga saffordiana* Pittier, en cuanto a la forma de sus estípulas, el raquis foliar terete, y los lóbulos de cáliz filiformes, pero no casi libres.

Esta especie presenta una variante en el Cerro Jefe con folíolos velutinos en el envés (*Systma & Anderson 1984*, MO), la cual se encuentra en un piso altitudinal mayor.

*Material representativo.* PANAMA. COLON: *Correa & Dressler 686* (MEXU). PANAMA: *Sytsma & Anderson 4442* (MO). SAN BLAS: *Herrera & Paredes 400* (MO). ZONA DEL CANAL: *Tyson et al. 4536* (MO).

**Inga flagelliformis** (Vell. Conc.) C. Martius, Flora 20(2): Beibl. 112. 1837. Basiónimo: *Mimosa flagelliformis* Vell. Conc., Fl. Flumin. 11: t. 27. 1831. TIPO: Brasil: *Vellozo, Fl. Flumin. 11: t. 27. 1831.*

*Inga jefensis* Liesner et D'Arcy, Ann. Missouri Bot. Gard. 75: 385, fig. 1. 1988. TIPO: Panamá: *Foster y Kennedy 1828* (isotipos, F, MO, US).

*Inga flagelliformis* es una especie muy variable, la cual tiende a tener la inflorescencia sobre tallos gruesos ya sin hojas. En Panamá y Colombia y en la mayoría del material de Brasil, las umbelas son axilares y solitarias a fasciculadas; sin embargo, en un ejemplar de Minas Gerais (*Duarte et al. 2765*, MO) las inflorescencias se presentan en tallos gruesos. La legumbre se presenta de casi recta (*Foster y Kennedy 1828*) a helicoidal (*Monsalve B. 988*).

Dentro de esta variación *Inga jefensis* Liesner et D'Arcy encaja muy bien, por lo que la incluimos bajo *I. flagelliformis*.

Esta especie está cercanamente emparentada al complejo de *Inga tenuistipula* Ducke, *I. lallensis* Spruce ex Benth., e *I. tessmannii* Harms, todas ellas con una flor muy similar y pedicelos más cortos o faltantes.

*Material representativo.* PANAMA. COCLE: *Porter et al. 4400* (MO). COLON: *Gentry et al. 8854* (MO). DARIEN: *Antonio & Hahn 4325* (MO). PANAMA: *Churchill & de Nevers 4968* (MO). COLOMBIA. CHOCO: *Duke 9580* (NY). VALLE: *Monsalve B. 988* (MO). BRASIL. (NORTE) AMAPA: *S. Mori et al. 15781* (K). AMAZONIA: *Cid et al. 77* (GH). PARA: *Ducke 10021* (US). (SUDESTE) MINAS GERAIS: *Duarte et al. 2765* (MO). RIO DE JANEIRO: *Luschnath s.n.* (MO).

**Inga flexuosa** Schldl., Linnaea 12: 559. 1838. TIPO: México. Veracruz: *Schiede 674* (isotipos, BR, G, GH).

*Inga pringlei* Harms, Repert. Spec. Nov. Regni Veg. 13: 526. 1915. TIPO: México. Veracruz: *Pringle 8125* (isotipos, A, BM, F, MEXU, MO, US).

Steudel creó un nuevo nombre, *Inga schiedeana*, para *Inga flexuosa* Schldl. aduciendo la ya existente *I. flexuosa* de Graham, sin embargo, este último nombre carece de descripción (nom. nud.) y sólo se encuentra en una lista en manuscrito (copia en MO), y por lo tanto no se considera válidamente publicado y no se puede crear un homónimo tardío.

La identidad de *Inga flexuosa* ha permanecido en duda desde Bentham (1875) y Standley (1922), ésto debido a la pobre descripción original de la parte fértil, así como lo estéril de los duplicados vistos; sin embargo, Britton & Rose (1928) la equiparan como *I. pringlei* Harms, lo cual parece posible por eliminación, considerando las pocas especies que hay en el área de la localidad del tipo, en los alrededores de Jalapa, Veracruz.

En *Inga flexuosa* las brácteas lineares muy largas que en ocasiones sobrepasan al cáliz, los botones florales con el cáliz abierto cuyos lóbulos son conniventes a todo lo largo formando un ápice rostrado a apiculado, así como la corola más pequeña la separan de *I. micheliana* Harms, especie que le es muy afín.

*Material representativo.* MEXICO. OAXACA: *Sousa et al. 9355* (MEXU). VERACRUZ: *Castilleja 66* (XAL).

**Inga glomeriflora** Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 50. 1922. TIPO: Brasil. Pará: *A. Ducke RB16609* (isotipos, BM, G, US).

*Inga golfodulcensis* Zamora, Brenesia 33: 107. 1991. TIPO: Costa Rica: *Hammel et al. 16963* (holotipo, CR; isotipos, MEXU, MO).

Esta especie se ubica en la sección *Bourgonia*, teniendo relaciones estrechas, pero es diferente a *Inga fanchoniana* Poncy de la Guayana Francesa, con la cual comparte varios caracteres, así ambas especies tienden frecuentemente a carecer de glándulas interfoliolares en los últimos pares de folíolos, sus hojas son glabras con ejes teretes, y las legumbres son circinado-espiraladas.

*Material representativo.* COSTA RICA. PUNTARENAS: *Hammel et al. 16963* (MO). PANAMA. PANAMA: *Dwyer et al. 7252* (US). COLOMBIA. META: *Callejas 7013* (MEXU). BRASIL. (NORTE) AMAZONIA: *Ducke 1207* (US). PARA: *Ducke RB16609* (US).

**Inga goldmanii** Pittier, Contr. U.S. Natl. Herb. 18: 198. 1916. TIPO: Panamá: *Goldman 1866* (holotipo, US).

Esta vistosa especie muestra grandes afinidades con *Inga davidsei* M. Sousa en Mesoamérica (véase ésta), de ella León (1966) nombró la serie *Goldmanianae* León basandose en las características florales, particularmente su robusto cáliz. En esta especie también son notables las glándulas foliolares supernumerarias (presentes también en *I. sierrae* Britton et Killip); este último carácter parece haber aparecido más de una vez en el género *Inga* ya que también está presente en *I. adenophylla* Pittier e *I. chocoensis* Killip ex T. S. Elias, especies claramente de la sección *Inga* que cuentan con la legumbre subterete y acordonada que es característica de la sección.

*Material representativo.* NICARAGUA. MATAGALPA: *Grijalva & Grijalva 1382* (MO). ZELAYA: *Ortiz 1255* (MO). COSTA RICA. ALAJUELA: *Holm & Iltis 951* (A). LIMON: *Lent 3690* (MO). PANAMA. BOCAS DEL TORO: *Dwyer 4464* (MO). COLON: *McPherson & Merello 8218* (MO). LOS SANTOS: *Duke 11904* (MO). PANAMA: *Knapp & Mallet 3932* (MO). VERAGUAS: *Dwyer 4310* (MO). ZONA DEL CANAL: *Nee 8924* (MO). COLOMBIA. VALLE: *Gentry 62901* (MO).

**Inga hayesii** Benth., Trans. Linn. Soc. London 30: 617. 1875. TIPO: Panamá: *Sutton Hayes 62* (holotipo, K).

Especie conocida hasta hace poco sólo de Panamá, pero con las colectas recientes ya se cuenta con material de Costa Rica y Colombia.

*Material representativo.* COSTA RICA. PUNTARENAS: *Poveda 658* (MO). PANAMA. DARIEN: *Stern et al. 964* (MO). PANAMA: *Dwyer 1484A* (MO). ZONA DEL CANAL: *Croat 14912* (MO). COLOMBIA. ANTIOQUIA: *Zarucchi et al. 4950* (MO). CHOCO: *Gentry & Brand 36969* (MO).

**Inga herrerae** Zamora, Brenesia 33: 107. 1991. TIPO: Costa Rica: *Herrera 1524* (holotipo, CR; isotipos, MEXU, MO).

Especie endémica de las montañas de Guanacaste, Costa Rica, característica por sus folíolos subcoriáceos a coriáceos y numerosos, y como Zamora (en prensa) ya ha apuntado sus peciólulos muy cortos. Es muy probable que el material en fruto de *Wilbur & Stone 10703* pertenezca a esta especie.

*Material representativo.* COSTA RICA. GUANACASTE: *Wilbur & Stone 10703* (NY).

**Inga heterophylla** Willd., Sp. Pl. ed. 4, 4: 1020. 1806. TIPO: Brasil: *Hoffmansegg s.n.* (holotipo, B-W, foto MO).

Para sinónimos véase Poncy (1985).

Especie que ha sido confundida en Mesoamérica con *Inga sertulifera* DC. *Inga heterophylla* Willd. se trata de una especie fundamentalmente de la Amazonía que marginalmente entra a Mesoamérica, en el Darién, en Panamá. Su inflorescencia es muy variable y va de un racimo corto corimboide hasta una umbela, lo que ha creado problemas en su identificación, ya que se le ha colocado generalmente en la sección *Leptinga* Benth., sección que en general varios autores la caracterizan por contar con inflorescencias en umbelas. Sin embargo Bentham (1845) claramente la define como de racimos umbeliformes.

*Material representativo.* PANAMA. DARIEN: *Knapp & Mallet 3091* (MO). TRINIDAD: *Broadway 5839* (MO). COLOMBIA. ANTIOQUIA: *Callejas et al. 2403* (MO). VENEZUELA. BOLIVAR: *Steyermark et al. 115591* (MO). SURINAM: *B. W. [Sur. For. Dept.] 3630* (MO). PERU. AYACUCHO: *Weberbauer 7541* (F). JUNIN: *Stein & Todzia 2395* (MO). MADRE DE DIOS: *R. Vásquez et al. 12409* (MO). LORETO: *Gentry et al. 39333* (MO). SAN MARTIN: *Klug 3521* (US). BOLIVIA: *Solomon 9489* (MO). BRASIL. (NORTE) AMAZONIA: *Byron & Lima 344* (MO). PARA: *W. R. Anderson 10662* (US). RONDONIA: *Forero & Wigley 7059* (MO). (SUDESTE) SAO PAULO: *Custodo & Gentry 4534* (MO). (SUR) PARANA: *Hatschbach 17964* (F).

**Inga hintonii** Sandw., Bull. Misc. Inform. 1937: 304. 1937 (como "*hintoni*"). TIPO: México. Edo. México: *Hinton 7617* (holotipo, K; isotipo, US).

*Inga davidsoniae* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 79. 1940. TIPO: Panamá: *Davidson 943* (holotipo, F; isotipos, MO, US).

*Inga nubigena* A. R. Molina, Ceiba 18: 99. 1971. TIPO: Honduras: *Molina R. 10656* (holotipo, F; isotipo, ENCB).

*Inga hintonii* es una especie muy variable, que se localiza en México y Mesoamérica de Nayarit, México a Chiriquí, Panamá; siempre en bosques húmedos de montaña, en ocasiones a más de 2,100 m de altitud. Su pariente más cercano es, sin duda, *I. micheliana* Harms, especie endémica a la vertiente del Golfo de México de Veracruz a Guatemala; de ella se distingue fundamentalmente por la flor más grande de *I. micheliana.*

*Material representativo.* MEXICO. CHIAPAS: *Sousa et al. 13178* (MEXU). JALISCO: *Magallanes 4445* (MEXU). EDO. MEXICO: *García R. 462* (MEXU). MICHOACAN: *Cházaro B. et al. 5585* (MEXU). NAYARIT: *Téllez V. 10021* (MEXU). OAXACA: *Cedillo T. 1820* (MEXU). GUATEMALA. SOLOLA: *Steyermark 47063* (F). HONDURAS. CORTES: *Molina R. 7251* (F). INTIBUCA: *Molina R. & Molina 24438* (F). LA PAZ: *Molina R. 6503* (F). MORAZAN: *Cruz R. 55* (MO). EL SALVADOR. SANTA ANA: *Molina R. & Montalvo 21494* (MO). SONSONATE: *Molina R. & Montalvo 21730* (NY). NICARAGUA. MATAGALPA: *Stevens 22142* (MO). ZELAYA: *Neill 3858* (MO). COSTA RICA. ALAJUELA: *Brenes 6805* (F). PUNTARENAS: *Koptur SK-115* (MO). SAN JOSE: *Stevens 13671* (MO). PANAMA. CHIRIQUI: *Stern et al. 1046* (MO).

**Inga ismaelis** M. Sousa, sp. nov. TIPO: México. Veracruz: km 5 camino Plan de Arroyo–Arroyo Alegre, Mpio. Hidalgotitlán, 17°15'N, 94°35'O, 140 m, 24 abr. 1974, *J. Dorantes et al. 3011* (holotipo, MEXU; isotipo, NY). Figura 4.

Arbores ex mediano procerae; rami juveniles ex modice flavescenti-ferrugineo-setosi hispidi. Folia (3–)4–5-jugata; stipulae 10–14 mm longae, triangulari-subulatae; foliola chartacea; rhachis foliaris alata, glandulis sessilibus vel fere sessilibus, urceolatis. Inflorescentiae racemosae corymboideae, rhachide florali brevi, bracteis elongatis persistentibus. Flores proximales pedicellati, distales fere sessiles; alabastra floralia calyce aperto; calyx tubulosus, lobulis longissimis triangulari-subulatis; corolla tubulosa, canescenti-villosa. Legumen usque ad 27 cm longum, complanatum, crassum, oblongum, sparse hispidum.

Arboles 6–20 m; ramas teretes, moderadamente setosas a híspidas con tricomas amarillos a ferrugíneos cuando jóvenes, posteriomente glabrescentes. Hojas (6–)8–10-folioladas; estípulas 10–14 mm, triangular-subuladas, persistentes; pecíolo 1–2 cm, angostamente alado; folíolos tenuemente

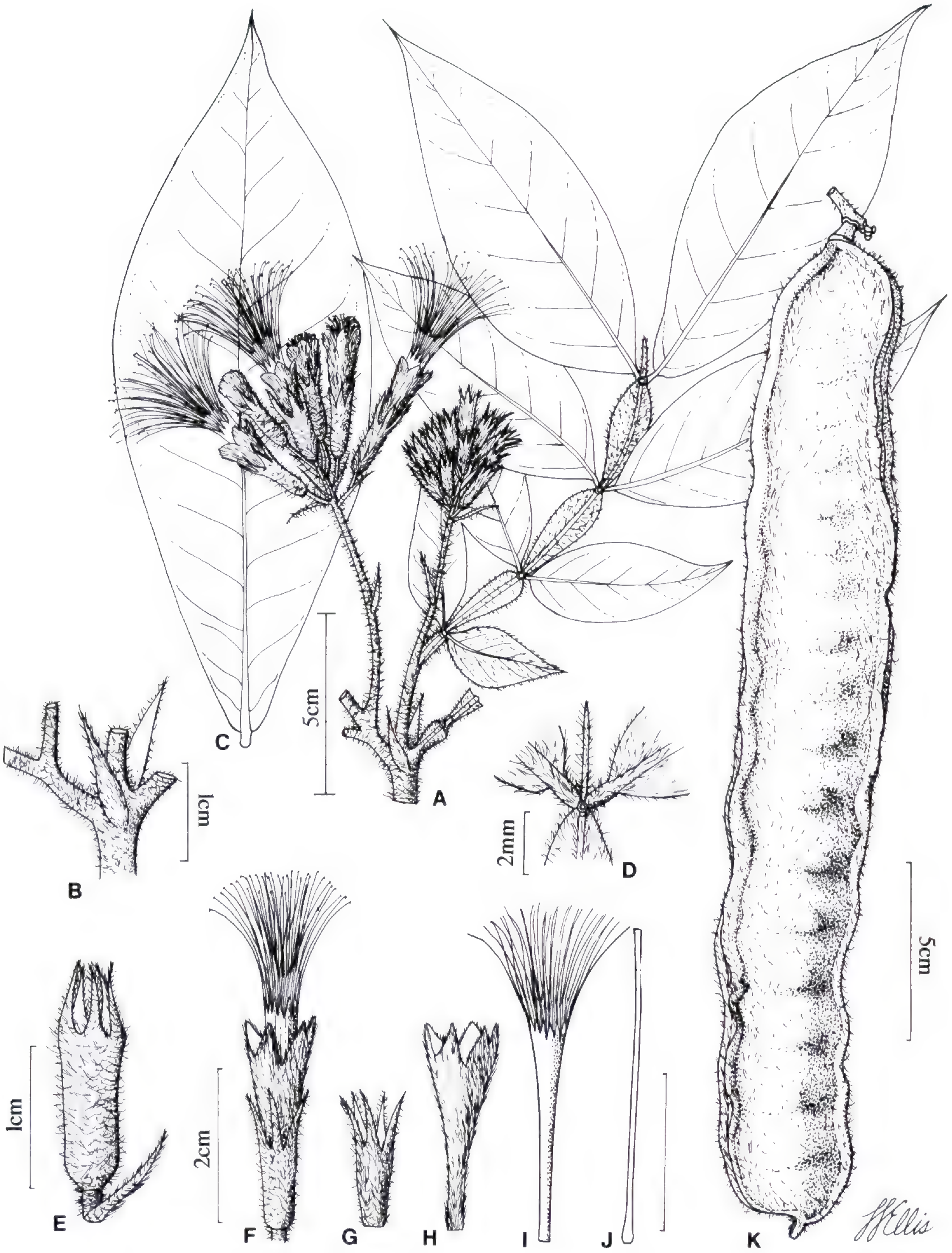


FIGURA 4. *Inga ismaelis* M. Sousa.—A. Rama con inflorescencias.—B. Detalle de estípulas.—C. Folíolo.—D. Detalle de glándula interfoliolar y ápendice. (Tomado de *J. Grimes et al. 2817.*)—E. Botón floral.—F. Flor.—G. Cáliz.—H. Corola.—I. Tubo estaminal.—J. Gineceo. (Tomado de *J. Dorantes et al. 3011.*)—K. Fruto. (Tomado de *J. Dorantes 3493.*)

discoloros, cartáceos, la base ligeramente asimétrica, cuneada a obtusa, el ápice agudo a cuspidado, el haz opaco, moderadamente a esparcidamente piloso, el envés pálido, moderadamente piloso, la nervadura primaria eglandular; par basal de folíolos 4.5–7.5 × 2.5–4.3 cm, ovados a elípticos, el par apical 15–20 × 5.5–8 cm, lanceolados o elípticos a oblanceolados; raquis foliar 5.5–16 cm, alado, el ala 5–11(–18) mm de ancho, generalmente elíptica, en ocasiones oblanceolada; glándulas interfoliolares en ocasiones ausentes, sésiles o casi sésiles, urceoladas cuando presentes, el cuerpo glandular 0.8–1 × 0.8–1 mm; apéndice 6–12 mm, setiforme. Inflorescencias en racimos corimboides, 1–2 fasciculadas; pedúnculo 5–8 cm, más o menos aplanado, sulcado, setoso; raquis floral 1.5–3 cm, las flores espaciadas proximalmente, congestas distalmente, las brácteas homomorfas 13–16 mm, triangular-subuladas a lanceolado-subuladas, generalmente con una estéril en el ⅓ superior del pedúnculo, persistentes. Flores pediceladas las proximales a casi sésiles las distales, el pedicelo hasta 9 mm, delgado; botones florales con el cáliz abierto, los lóbulos erectos no conniventes; cáliz 16–21 mm, tubular, estriado, piloso, sin escotaduras, los lóbulos 5–7 mm, triangular-subulados; corola 23–27 mm, tubular a subturbinada, blanca, canescente vellosa; tubo estaminal inserto a cortamente exerto, blanco. Legumbre ca. 27 × 3.5 × 0.6 cm, aplanada, más o menos derecha, linear-oblonga, sésil, rostrada en el ápice, esparcidamente híspida, las valvas aplanadas, inconspicuamente nervadas, las suturas prominentes, los márgenes de las suturas 1-sulcados.

*Distribución y hábitat.* Del área de Uxpanapa en el sur de Veracruz y del área de Tuxtepec en el norte de Oaxaca, México, en sitios riparios en selvas altas perennifolias con *Dialium*, *Ormosia* (Leguminosae), *Licania* (Chrysobalanaceae), y *Brosimum* (Moraceae), en suelos profundos, arcillosos, amarillentos, en afloramientos de rocas calizas en altitudes entre los 100 a 150 m. Florece en abril y fructifica en septiembre.

*Nombres vernáculos.* Chacaruite, guagenecuil de la montaña, vaina, jinicuil.

*Usos.* Los frutos maduros son comestibles.

*Paratipos.* MEXICO. OAXACA: Distr. Tuxtepec, Mpio. Jalapa de Díaz, Río Uluapan, carr. Jalapa de Díaz a San Bartolomé Ayautla, *I. Calzada 16860* (MEXU). VERACRUZ: Mpio. Jesús Carranza, 20 km S del Poblado 2, 3 4 km S del entronque de la terracería La Laguna Boca del Monte en el camino al N del Poblado 2, *J. Grimes 2817* (MO, NY, TEX). Mpio. Hidalgotitlán, 4 km camino a La Laguna, *M. Avendaño 40* (MEXU, XAL); km 0 2 del camino Plan de Arroyos–Alvaro Obregón, 17°15′N, 94°40′O, *J. Dorantes et al. 2806* (NY, XAL); km 4–5 caminito que cruza la carretera La Laguna, *Dorantes 3493* (MEXU, XAL); 1 km al N Campamento Hermanos Cedillo, 17°16′N, 94°37′O, *M. Vázquez et al. 385* (ENCB, NY, WIS, XAL).

*Inga ismaelis* está emparentada con *I. setosa* Don e *I. pavoniana* Don, siendo más cercana a *I. setosa* Don del Perú, de ésta difiere *I. ismaelis* por tener las glándulas del raquis foliar sésiles o casi sésiles, las flores más grandes, las estípulas mucho más largas que anchas así como las brácteas alargadas en vez de cordatas. El largo de los lóbulos del cáliz sólo se equipara al de los de *I. velutina* Willd. del Amazonas.

Esta especie se dedica a Juan Ismael Calzada (1950–), colector de las selvas de México, quien trabajó para el proyecto Flora de Veracruz, cuyo personal es el que fundamentalmente ha colectado a esta especie.

**Inga jinicuil** Schldl., Linnaea 12: 559–560. 1838.
TIPO: Costa Rica: *Jiménez & Zúñiga 815* (holotipo, CR; isotipo, MO).

Especie conocida de la vertiente Pacífica, San José, Costa Rica, y del Cerro Pierre en el Darién en Panamá. Sus relaciones en Mesoamérica parecen ser con *Inga calderonii*, difiriendo de ella en varios caracteres; también muestra, aunque no tan cercanamente, relaciones con la sección *Vulpinae* Benth. De este último grupo *Inga jimenezii* difiere fundamentalmente por los lóbulos cortos del cáliz.

*Material representativo.* COSTA RICA. SAN JOSE: *Jiménez & Zúñiga 815* (MO). PANAMA. DARIEN: *Gentry 1612* (BM).

**Inga jinicuil** Schldl., Linnaea 12: 559–560. 1838.
TIPO: México. Veracruz: *Schiede 675* (isotipos, CAS, G, GH, MO).

*Inga jinicuil*, a pesar de disponerse a partir del trabajo de León (1966) con nuevas y numerosas colectas, se mantiene aparte, sin que pueda incluirse con *I. paterno* Harms; sus diferencias son tanto en caracteres vegetativos, florales, como en los hábitats. *Inga jinicuil* se encuentra en un piso altitudinal mayor que el de *I. paterno* (véase clave de especies).

*Material representativo.* MEXICO. CHIAPAS: *Martínez S. 22146* (MEXU). MICHOACAN: *Emrick 38* (F). Morelos: *Cordero C. 2* (MEXU). OAXACA: *Rivera R. 1491* (MEXU). PUEBLA: *Miranda G. 1435* (MEXU). VERACRUZ: *Calzada 1969* (MEXU). GUATEMALA. BAJA VERAPAZ: *Lundell & Contreras 20885* (LL).

**Inga lacustris** M. Sousa, sp. nov. TIPO: México. Veracruz: costa N de la Punta Levisa, en la Laguna de Sontecomapan, Mpio. Catemaco, 18°32′N, 95°11′O, 15 abr. 1973, *F. Menén-*

*dez L. 144* (holotipo, MEXU; isotipos, MEXU, MO, XAL). Figura 5.

Arbores parvae; rami juveniles sparse tomentosi cito glabrescentes. Folka 2-jugata; stipulae 9–12 mm longae, triangulari-subulatae; foliola ex lanceolata elliptica apice ex acuminato cuspidata; rhachis foliaris ex marginata alata glandulis sessilibus patellatis. Inflorescentiae racemosae floribus distantibus; bracteae sensim heteromorphae. Flores pedicellati; alabastra floralia attenuato-obtusa, calyce aperto; calyx tubulosus, laevis, marginatus; corolla tubulosa, sparse canescenti-sericea; tubus stamineus longe exsertus. Legumen (immaturum) parvum, complanatum, oblongum, sparse hispidulum.

Arboles 3–7 m; ramas teretes a tenuemente anguladas, esparcidamente tomentosas cuando jóvenes, pronto glabras y rojizo brillante. Hojas 4-folioladas; estípulas 9–12 mm, triangular-subuladas, persistentes; pecíolo 0.7–2.2 cm, terete a alado; folíolos tenuemente discoloros, cartáceos a subcoriáceos, la base simétrica cuneada a ligeramente cordata, el ápice acuminado a cuspidado, el haz brillante a opaco, glabro, el envés algo brillante a opaco, glabrescente, la nervadura primaria eglandular; par basal de folíolos 3.5–9.5(–14) × 1.8–4(–6) cm, lanceolados a elípticos, el par apical (8–)18–23(–27.5) × (3–)5–6.5(–8) cm, elípticos; raquis foliar 2.5–5 cm, marginando a alado, el ala 5–9 mm de ancho, oblanceolada; glándulas interfoliolares sésiles, pateniformes, el cuerpo glandular, ca. 1 × 1 mm; apéndice 4 mm, setiforme, pronto caduco. Inflorescencias en racimos solitarios; pedúnculo 4.5–9 cm, estriado, esparcidamente tomentoso a glabrescente; raquis floral 5–7.5 cm, las flores esparcidas, particularmente las proximales, las brácteas gradualmente heteromorfas, 1–4 mm, las proximales cóncavas ovado-lanceoladas, las distales estipitado-cuculadas, en ocasiones con una estéril del ½ al ápice del pedúnculo, persistentes. Flores proximales pediceladas, el pedicelo esbelto hasta 3.5 mm, las distales casi sésiles; botones florales con el cáliz abierto y los lóbulos imbricados, atenuado-obtusos; cáliz 3–9 mm, tubular, liso, esparcidamente tomentoso, seríceo a glabrescente, con escotaduras, los lóbulos ca. 1 mm, triangular-cuspidados; corola 13–15 mm, tubular, blanca, esparcidamente canescente sericea; tubo estaminal largamente exerto, blanco. Legumbre (inmadura) 4.5–7.6 × 2.5–3.2 × 0.2 cm, aplanda, derecha, oblonga, truncada en la base, apiculada en el ápice, esparcidamente hispídula, las valvas aplanadas, las suturas onduladas, marginadas.

*Distribución y hábitat.* Sólo conocida de la orilla N de la Laguna de Sontecomapan, en la región volcánica de Los Tuxtlas en Veracruz, México, en una selva perennifolia que está delimitada por manglares de *Laguncularia racemosa*, sobre suelos arenosos; al nivel del mar. Esta especie está muy restringida en área y se limita a unos cuantos árboles. Florece en abril y junio, inicia la fructificación en abril y aún tiene frutos inmaduros a fines de julio.

*Paratipos.* MEXICO. VERACRUZ: Mpio. Catemaco, Punta Levisa, Laguna de Sontecomapan, *I. Calzada 987* (MEXU), *s.n.* [15 abr. 1973] (MEXU), *1805* (MEXU), *11658* (MEXU, XAL), *12004* (MEXU, MO, XAL); Rancho Levisa, en Punta Levisa, orilla N Laguna de Sontecomapan, *M. Sousa & I. Calzada 13021* (MEXU, MO).

*Inga lacustris* está emparentada con *I. cookii* Pittier; sin embargo, difiere de ella, particularmente en su pelosidad, estípulas y glándulas interfoliolares, así como brácteas florales y pelosidad de la legumbre. El epíteto se emplea para hacer énfasis en el tan particular hábitat, de una especie en inminente peligro de extinción.

**Inga latibracteata** Harms, Repert. Spec. Nov. Regni Veg. 19: 64. 1923. TIPO: México. Veracruz: *Pringle 8159* (isotipos, F, MEXU, US).

*Inga borealis* T. S. Elias, Phytologia 14: 208. 1967. TIPO: México. San Luis Potosí: *King 4275* (holotipo, NY; isotipos, F, MICH, TEX, US).

Para demás sinónimos, excepto *I. zacuapanica* Harms, véase León (1966).

Especie muy variable que se caracteriza por tener flores con una bráctea subyacente muy bien desarrollada que llega a proporciones foliáceas en *Inga borealis* que representa el extremo de variación de este carácter, así como el extremo norte de distribución de la especie. El otro extremo de variación sería *I. oerstediana* Benth., de la cual *I. latibracteata* representa una variación geográfica; sin embargo, creo deben mantenerse separadas por el momento. Existen varias formas intermedias entre esta especie e *I. vera* Willd. que interpretamos como híbridos; el nombre más antiguo que corresponde a este híbrido propuesto es *I. xalapensis* Benth. (véase a éste para mayores detalles).

*Material representativo.* MEXICO. CHIAPAS: *Ton 5576* (MEXU). OAXACA: *Torres C. & Ramírez 8461* (MEXU). PUEBLA: *Campos V. & Toris A. 204* (MEXU). QUERETARO: *Fernández N. 3891* (ENCB). SAN LUIS POTOSI: *King 4275* (TEX). VERACRUZ: *Velázquez L. 171* (MO).

**Inga latipes** Pittier, Contr. U.S. Natl. Herb. 18: 183. 1916. TIPO: Costa Rica: *Tonduz 13056* (holotipo, US; isotipos, BM, K, NY).

Esta especie es sólo conocida de las áreas montañosas de la Provincia de Cartago en Costa Rica.

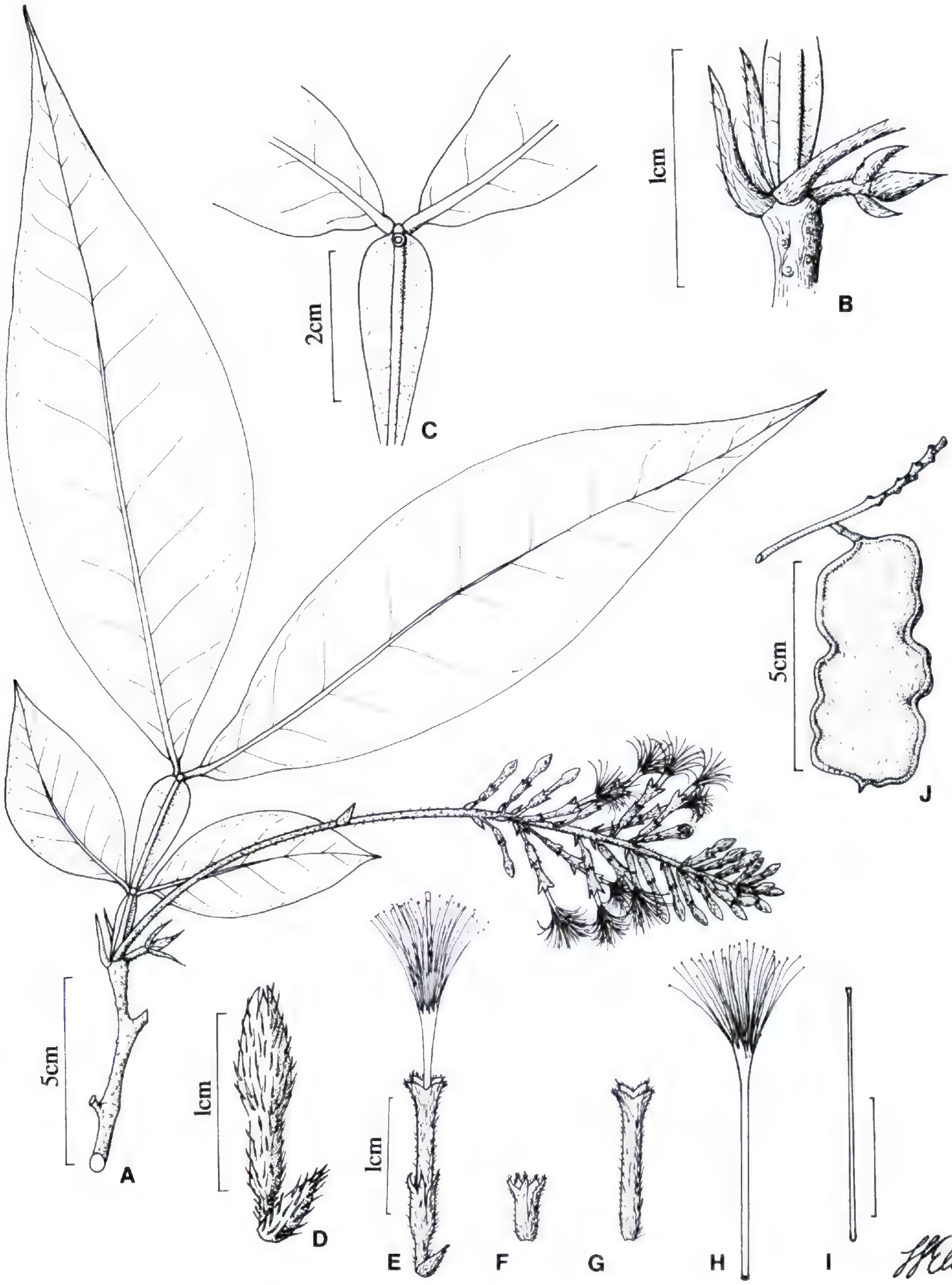


FIGURA 5. *Inga lacustris* M. Sousa.—A. Rama con inflorescencia. -B. Detalle de estípulas.—C. Glándula interfoliolar.—D. Botón floral.—E. Flor.—F. Cáliz.—G. Corola.—H. Tubo estaminal.—I. Gineceo. *F. Menéndez L. 144.*—J. Fruto. (Tomado de *Sousa 13021.*)

A pesar de estar muy cerca de *I. punctata* Willd., no creo que se pueda sinonimizar con ella, como sugirió pero no hizo León (1966). *Inga latipes* difiere de *I. punctata* tanto en caracteres vegetativos (glándulas interfoliolares muy promimentes) y florales (flores pediceladas y el cáliz casi glabro) como en el fruto (mucho más grande). Por su cáliz casi glabro y su fruto de grandes dimensiones se parece más a *I. leiocalycina* Benth., pero *I. latipes* tiene hojas de menor tamaño, 6-folioladas, las glán-

dulas interfoliolares más grandes, además de las flores pediceladas.

*Material representativo.* COSTA RICA. CARTAGO: *Lent 2111* (F).

**Inga laurina** (Sw.) Willd., Sp. Pl. ed. 4, 4: 1018. 1806. Basiónimo: *Mimosa laurina* Sw., Prodr. 85. 1788. TIPO: St. Kitts: *Masson s.n.* (holotipo, BM, no localizado).

*Inga fagifolia* (L.) Willd. ex Benth., Trans. Linn. Soc. London 30: 607. 1875. Basiónimo: *Mimosa fagifolia* L., Sp. Pl. 516. 1753, non *Inga fagifolia* Don, Gen. Hist. 2: 391. 1832. [= *I. ruiziana* Don].

A pesar de que el basiónimo más antiguo de esta especie es el de Linneo no se le puede emplear como lo hizo León (1966), ya que Willdenow (véase descripción de *Inga semialata*) no formalizó el cambio a *Inga*, siendo hasta Bentham (1875) que lo hizo, pero antes G. Don (1832) lo empleó para otro taxon.

Sobre si el material de las Antillas difiere significativamente de él del continente americano, León (1966) da una buena discusión del problema y concuerdo con él, ya que en términos generales la diferencia se reduce a un sólo carácter: el tubo estaminal exerto o inserto.

*Material representativo.* MEXICO. CHIAPAS: *Sousa et al. 12908* (MEXU). GUERRERO: *Soto N. et al. 5180* (MEXU). JALISCO: *Santana & Guzmán 3330* (WIS). NAYARIT: *Flores F. et al. 919* (MEXU). OAXACA: *Torres C. & Martínez S. 4817* (MEXU). GUATEMALA. ALTA VERAPAZ: *Contreras 4553* (MEXU). CHIQUIMULILLA: *Clarke 19918-1* (TEX). ESCUINTLA: *Hayes s.n.* (GH). RETALHULEU: *Standley 87254* (F). HONDURAS. LEMPIRA: *Molina R. 24147* (F). EL SALVADOR. AHUACHAPAN: *Standley & Padilla B. 2836* (GH). LA PAZ: *Flores 283* (MO). SAN VICENTE: *Standley 21744* (F). NICARAGUA. ZELAYA: *Little 25397* (F). COSTA RICA. GUANACASTE: *Herrera 1460* (MO). HEREDIA: *Hartshorn 1325* (MO). PANAMA. COCLE: *Dwyer 2045* (MO). HERRERA: *Allen 4037* (MO). LOS SANTOS: *Croat 9753* (MO). PANAMA: *Allen 817* (BM). VERAGUAS: *Tyson 6074* (MO). ZONA DEL CANAL: *Croat 6119* (MO). REPUBLICA DOMINICANA: *Valeur 716* (F). PUERTO RICO: *Little 13465* (F). ST. THOMAS: *Britton & Marble 1226* (F). TORTOLA: *Britton & Shafer 716* (F). ANTIGUA: *Rose et al. 3457* (F). MARTINICA: *Stehle 5690* (F). TRINIDAD: *Sieber 120* (F). VENEZUELA. BOLIVAR: *Liesner & González 5501* (MO). DELTA AMACURO: *Blanco 250* (MO). GUAYANA: *E. Cardona 2157* (MO). TACHIRA: *Steyermark et al. 120408* (MO). ECUADOR. NAPO: *Neill et al. 7228* (MO). PASTAZA: *Palacios & Neill 627* (MO). BOLIVAR: *Little 6737* (MO). PERU. LORETO: *Vásquez & Jaramillo 10973* (MO). MADRE DE DIOS: *Núñez 5765* (MO). URAYALI: *Gentry & Díaz 58583* (MO). BRASIL. (NORTE) PARA: *Cavalcante & Silva 2903* (MO). (NORDESTE) BAHIA: *Harley et al. 15329* (MO). MARANHAO: *Froes 11688* (MO). (CENTRO OESTE) DISTRITO FEDERAL: *Irwin & Soderstrom 6168* (MO). GOIAS: *Heringer 14770* (MO). (SUDESTE) RIO DE JANEIRO: *Pereira & Duarte 4498* (MO). (SUR) PARANA: *Hatschbach 43201* (MO). ARGENTINA. CORRIENTES: *Schinini & Vanni 15506* (MO).

**Inga leiocalycina** Benth., London J. Bot. 4: 598. 1845. TIPO: Guyana: *Schomburgk 829* (lectotipo, designado por Poncy (1985), P: isolectotipos, BM, F, G, K).

*Inga yunckeri* Standley, Field Mus. Nat. Hist., Bot. Ser. 9: 296. 1940. TIPO: Honduras: *Yuncker et al. 8805* (holotipo, F; isotipos, BM, G, K, MO, US).

Especie hasta hace poco sólo conocida de Brasil y las Guayanas (Poncy, 1985), pero en realidad se extiende hasta el sur de México. En Mesoamérica ya tenía un nombre: *Inga yunckeri* Standley como endémica de Honduras (León, 1966). *Inga leiocalycina* es en general una especie bastante homogénea, la cual debido a su similitud con *I. punctata* Willd. (véase ésta) se le ha identificado como tal (véanse también comentarios de Poncy, 1985).

Poncy (1985) sinonimiza bajo esta especie a *Inga strigillosa* Spruce ex Benth. (Trans. Linn. Soc. London 30: 612. 1875) e *I. dumosa* Benth. (loc. cit., 30: 612. 1875), lo cual no me parece justificable, ya que estas dos presentan los cálices pelosos que se parecen más a *I. punctata* Willd.

*Inga leiocalycina* es un elemento amazónico de selvas altas perennifolias que se extiende en las áreas bajas cálido húmedas de Norte y Sudamérica.

*Material representativo.* MEXICO. OAXACA: *Wendt 4424* (MEXU). VERACRUZ: *Wendt et al. 3771* (MEXU). GUATEMALA. EL PETEN: *Contreras 6008* (LL). IZABAL: *Marshall et al. 445* (NY). HONDURAS. ATLANTIDA: *Yuncker et al. 8805* (MO). CORTES: *García 50* (MO). MORAZAN: *Bourdeth 53* (MO). NICARAGUA. RIO SAN JUAN: *Moreno 25549* (MO). ZELAYA: *Standley 19361* (F). COSTA RICA. HEREDIA: *Hartshorn 1181* (F). LIMON: *Gómez P. et al. 22813* (MO). PANAMA. BOCAS DEL TORO: *McPherson & Sanders 14717* (MO). COLON: *Nee 7272* (MO). SAN BLAS: *McPherson 12733* (MO). COLOMBIA. VALLE: *Hilty J-39* (US). VENEZUELA. AMAZONAS: *Lister & Colchester 2504* (K). BOLIVAR: *Maguire et al. 53802* (US). DELTA AMACURO: *Marcano-Berti et al. 38-1-77* (G). GUYANA: *Hitchcock 17158* (US). SURINAME: *Prance et al. 55726* (MO). GUAYANA FRANCESA: *Poncy 133* (MO). PERU. AMAZONAS: *Kayap 277* (MO). LORETO: *R. Vásquez et al. 7906* (MO). PASCO: *D. Smith 1905* (MO). BOLIVIA. PANDO: *Prance et al. 6470* (NY). BRASIL. (NORTE) AMAZONIA: *Prance et al. 13707* (F). PARA: *Fróes 32210* (US). (CENTRO OESTE) MATO GROSSO: *Berg et al. P18440* (MO).

**Inga leonis** Zamora, Brenesia 33: 111. 1991. TIPO: Costa Rica: *Lent 3541* (holotipo, CR; isotipos, F, MEXU).

Esta especie está en el complejo de *Inga villosissima* Benth., *I. dasycarpa* M. Sousa, *I. te-*

*nella* M. Sousa, *I. chiapensis* Miranda ex M. Sousa, e *I. sierrae* Britton et Killip. Es más cercana a *I. chiapensis*, de la cual difiere en sus hojas, en sus frutos, así como el color de la corola.

*Material representativo.* COSTA RICA. ALAJUELA: *Lent 3541* (MEXU). HEREDIA: *Utley & Utley 2825* (F). LIMON: *Hammel et al. 17061* (MO). PANAMA. BOCAS DEL TORO: *McPherson 9855* (MO). COCLE: *Sytsma 1883* (NY). CHIRIQUI: *McPherson 12830* (MO).

**Inga litoralis** Zamora, Brenesia 33: 115. 1991. TIPO: Costa Rica: *Burger et al. 10572* (holotipo, CR; isotipos, BM, F, MEXU, NY).

Esta especie, sólo conocida del tipo, está cercanamente emparentada a *Inga tenella* M. Sousa, de la cual difiere por la pelosidad del cáliz, el pedúnculo floral, y la forma de las brácteas, además de que desconocemos su fruto.

*Material representativo.* COSTA RICA. PUNTARENAS: *Burger et al. 10572* (MEXU).

**Inga longispica** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 497. 1937. TIPO: Costa Rica: *Brenes 6371* (holotipo, F).

Especie poco conocida que hasta hace poco se colectó en Panamá y Colombia.

*Material representativo.* COSTA RICA. ALAJUELA: *Skutch 3705* (A). PUNTARENAS: *Koptur & Guindon SK-217* (MO). SAN JOSE: *Utley 5752* (MEXU). PANAMA. BOCAS DEL TORO: *McPherson 8408* (MO). COLOMBIA. VALLE DE CAUCA: *Monsalve B. 1730* (MEXU).

**Inga micheliana** Harms, Repert. Spec. Nov. Regni Veg. 13: 525. 1915. TIPO: Guatemala: *Heyde & Lux 3319* (isotipos, GH, K, MO, US).

Esta especie tiene como parientes cercanos por un lado a *Inga flexuosa* Schldl. y por otro a *I. hintonii* Sandw. (véanse discusiones de éstas).

En *Inga micheliana* el raquis foliar es más frecuentemente terete, pero en ocasiones se presenta alado, como lo es en el tipo.

*Material representativo.* MEXICO. CHIAPAS: *Miranda G. 7116* (MEXU). GUATEMALA. CHIQUIMULA: *Hughes 1461* (MEXU). QUICHE: *Heyde & Lux 3319* (GH).

**Inga mortoniana** Léon, Ann. Missouri Bot. Gard. 53: 351, fig. 6. 1966. TIPO: Costa Rica: *A. Smith 1230* (holotipo, NY; isotipos, F, US).

Esta especie está muy relacionada a *Inga acrocephala* Steudel, particularmente con la variante de inflorescencias capituliformes, pero con flores más grandes: cáliz 5–7 mm de largo en *I. mortoniana* (versus 1.5–3 mm en *I. acrocephala*) y corola (7–)9–12 mm de largo (versus 6–9 mm), la corola más grande de menos de 2 veces el largo del cáliz (versus. la corola de 2.2–3.5 veces el largo que el cáliz); *I. mortoniana* tiende también a tener un cáliz glabrescente a esparcidamente canescente seríceo. Ambas especies característicamente tienen campos glandulares en los lóbulos del cáliz, que en cálices maduros adquieren un aspecto calloso. En fruto ambas especies, hasta donde puedo ver, son indiferenciables, y de hecho, *Inga mortoniana* podría pasar a una categoría infraespecífica de *I. acrocephala*, pero debido a las antedichas diferencias florales creo prudente mantenerlas aparte. En general *Inga mortoniana* habita en un piso altitudinal mayor que *I. acrocephala*.

El material de Venezuela (*Steyermark 91992*) tiene la corola más pequeña pero el cáliz grande y glabrescente.

*Material representativo.* COSTA RICA. ALAJUELA: *Skutch 3780* (MO). PUNTARENAS: *Hartshorn 1790* (NY). VENEZUELA. DISTRITO FEDERAL: *Steyermark 91992* (NY).

**Inga mucuna** Walp. et Duchass., Ann. Bot. Syst. 2: 459. 1852. TIPO: Panamá: *Duchassaing 81* (isotipo, GH).

Coincidimos con León (1966) en que *Inga mucuna* está estrechamente emparentada a *I. fastuosa* (Jacq.) Willd., pero a pesar de las nuevas colectas hechas posteriormente al trabajo de León (1966), estos taxa, aún se sostienen aparte. Por otro lado *Inga vera* Griseb. ex Benth., que León (1966) apuntó como especie endémica de Trinidad relacionada con *I. mucuna*, se puede considerar sinónimo de *I. fastuosa*. Así tenemos *I. fastuosa* de Trinidad, Venezuela, y las Guayanas e *I. mucuna* de Panamá y Colombia.

*Material representativo.* PANAMA. COLON: *Nee 9101* (MO). DARIEN: *Kennedy 2899* (MO). PANAMA: *Duchassaing 81* (GH). SAN BLAS: *Dwyer 6847* (MO). ZONA DEL CANAL: *Croat 12234* (MO), COLOMBIA. ANTIOQUIA: *Brand & Cogollo 214* (MO). CHOCO: *Juncosa 2508* (MO).

**Inga multijuga** Benth., Trans. Linn. Soc. London 30: 615. 1875. TIPO: Panamá: *Sutton Hayes 645* (lectotipo, designado aquí, K, el colector y colecta lo dió Pittier en 1929, pero no el herbario; isolectotipos, BM, BR, G, P).

Bajo este nombre se ha aglutinado desde la descripción original, una amplia variación que el mismo Bentham (1875) reconoció; posteriormente Pit-

tier (1916) segregó *Inga aestuariorum* Pittier, la cual León (1966) volvió a unir pero que aquí considero aparte (véase discusión de *I. aestuariorum*). También se ha determinado bajo *I. multijuga*, material recientemente colectado que al estudiarlo lo estoy describiendo como *I. cuspidata* M. Sousa (véase ésta).

*Material representativo.* COSTA RICA. LIMON: *Robles 1889* (MO). PUNTARENAS: *Khan et al. 501* (BM). PANAMA. COLON: *Holdridge 6512* (MO). DARIEN: *Garwood et al. 2048A* (BM). SAN BLAS: *Lewis et al. 194* (MO). ZONA DEL CANAL: *Croat 5403* (MO). VENEZUELA. TACHIRA: *Liesner et al. 9621* (MO).

**Inga oerstediana** Benth., Bot. Herald 117. 1853. TIPO: Panamá: *Seemann 1688* (lectotipo, designado aquí, BM, el colector lo dió Pittier en 1929, pero no el herbario ni la colecta).

*Inga endlicheri* (Kuntze) J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13: 23. 1943. Basiónimo: *I. fasciculata* Poeppig, Nov. Gen. Sp. Pl. 3: 79. 1845, non Willd. 1806. TIPO: Perú: *Poeppig 1340* (holotipo, NY).

*Inga minutula* (Schery) T. S. Elias, Phytologia 14: 211. 1967. Basiónimo: *I. edulis* C. Martius var. *minutula* Schery, Ann. Missouri Bot. Gard. 37: 209, fig. 81. 1950. TIPO: Panamá: *Allen 968* (holotipo, MO; isotipos, F, US).

Para demás sinónimos véase León (1966).

*Inga oerstediana* es una especie muy variable, fundamentalmente de las montañas mesoamericanas, donde frecuentemente es empleada como sombra de café. Sin embargo existen poblaciones de baja altitud en las que en ocasiones varia la pelosidad de sus flores hacia tonos cinéreos en vez de ferrugíneos. Esta variación ha sido elevada a especie (*I. minutula* (Schery) T. S. Elias), lo que no parece justificable mantener; podría considerarse como variedad, pero bajo *I. oerstediana* en vez de *I. edulis* C. Martius. Este complejo, al noreste montañoso de su distribución, adquiere una bráctea de grandes proporciones y así tenemos *I. latibracteata* Harms, especie que mantenemos por la combinación de caracteres que presenta (véase discusión de *I. latibracteata*). En Sudamérica *I. oerstediana* se parece mucho, particularmente en sus flores y frutos, a *I. scabriuscula* Benth. de las Guayanas, el Territorio Delta Amacuro de Venezuela, y la Amazonía de Brasil, pero difiere por las hojas (la forma de los folíolos, nervaduras, y pelosidad). A su vez *I. scabriuscula* es similar a *I. edulis* (véase discusión bajo *I. edulis*).

Las especies de este grupo de *Inga* de la sección *Inga* con glándulas interfoliolares prominentes forman una serie interconectada teniendo en un extremo *I. edulis* y en otro *I. latibracteata*, pero creo que deben mantenerse separadas para su mejor entendimiento.

*Material representativo.* MEXICO. CHIAPAS: *Sousa et al. 13179* (MEXU). GUERRERO: *Soto N. 5226* (MEXU). OAXACA: *Breedlove 25129* (MO). TABASCO: *Hernández X. & Segalen 239* (MEXU). VERACRUZ: *Dorantes et al. 2579* (MO). BELICE. STANN CREEK: *Gentle 3020* (A). GUATEMALA. ALTA VERAPAZ: *Standley 89677* (F). BAJA VERAPAZ: *Harmon & Dwyer 3151* (MO). CHIMALTENANGO: *Standley 64478* (F). ESCUINTLA: *Standley 63873* (F). QUEZALTENANGO: *Standley 87910* (F). SACATEPEQUEZ: *Standley 63336* (F). SUCHITEPEQUES: *Hughes et al. 1381* (MEXU). HONDURAS. ATLANTIDA: *Yuncker 4922* (MO). COLON: *Bangham 250* (F). COMAYAGUA: *Molina R. 8067* (F). CORTES: *Allen 6457* (F). EL PARAISO: *L. O. Williams & Molina R. 11993* (MO). MORAZAN: *Rodríquez M. s.n.* (MO). OLANCHO: *Mejía 163* (MO). YORO: *Hagen & Hagen 1117* (F). EL SALVADOR. AHUACHAPAN: *Standley & Padilla B. 2733* (F). LA LIBERTAD: *Carlson 206* (F). SAN SALVADOR: *Calderón 1564* (GH). SANTA ANA: *L. O. Williams et al. 15168* (F). NICARAGUA. CARAZO: *Neill 246* (MO). CHONTALES: *Stevens 22601* (MO). GRANADA: *Sandino & McKearin 416* (MO). ESTELI: *Sousa et al. 12993* (MEXU). JINOTEGA: *Sandino 82* (MO). MATAGALPA: *Vincelli 336* (MO). RIO SAN JUAN: *Riviere 299* (MO). ZELAYA: *Stevens 12335* (MO). COSTA RICA. ALAJUELA: *Brenes 5495* (CR). CARTAGO: *Hammel & Grayum 16615* (MO). HEREDIA: *Hartshorn 943* (MO). LIMON: *Gómez P. et al. 22763* (MO). PUNTARENAS: *Liesner 2208* (MO). SAN JOSE: *Barringer & Christenson 3286* (F). PANAMA. COCLE: *Lao 282* (MO). COLON: *McPherson 7930* (MO). CHIRIQUI: *Hufft 1845* (MO). DARIEN: *Stern et al. 627* (MO). PANAMA: *Dwyer 1778* (MO). SAN BLAS: *Sugden 380* (MO). ZONA DEL CANAL: *Allen 1972* (MO). COLOMBIA. ANTIOQUIA: *Uribe-Uribe 2075* (US). CHOCO: *Gentry & Fallen 17712* (MO). MAGDALENA: *White & Alverson 653* (MO). NORTE DE SANTANDER: *Cuatrecasas et al. 12215* (MO). VALLE: *Devia 257* (MO). VENEZULA. CARACHE: *Benítez de Rojas 1929* (MO). LARA: *Davidse & González 20963* (MO). MERIDA: *Breteler 3215* (MO). MIRANDA: *González & Ortega 1360* (MO). ECUADOR. EL ORO: *Steyermark 53948* (MO). ESMERALDAS: *Litte & Dixon 21074* (MO). PERU. AMAZONAS: *Tunqui 442* (MO). CUZCO: *Núñez et al. 8249* (MO). MADRE DE DIOS: *Gentry 43696* (MO). PASCO: *Smith et al. 5415* (MO).

**Inga paterno** Harms, Repert. Spec. Nov. Regni Veg. 13: 419. 1914. TIPO: Guatemala. Santa Rosa: Barberena, 1,000 m, July 1893, *Heyde & Lux 3280* (lectotipo, redesignado aquí, US; isolectotipos, G, GH).

*Inga radians* Pittier, Contr. U.S. Natl. Herb. 18: 178. 1916. TIPO: México. Chiapas: *Cook 805* (holotipo, US).

Harms (1914) al describir a *Inga paterno* no designó holotipo y la basó en varias colectas, sintipos; de ellos León (1966) escogió como tipo a *Preuss 1387*, ejemplar que ya para esas fechas

había sido destruido en B, y en vista que no se han encontrado duplicados en otros herbarios, considero la lectotipificación de León fue inapropiada y designo aquí el lectotipo en base a un isosintipo existente, en vista que los otros sintipos de B también fueron destruidos.

Especie muy afín a *Inga cinnamomea* Spruce ex Benth. de la Amazonia, pero lo suficientemente diferenciada para considerarla en una sola entidad con *I. cinnamomea*.

Se cultiva ampliamente en México y Centroamérica por lo apetecido de la pulpa de su fruta, la cual es muy popular desde épocas precolombinas y que se vende ampliamente en mercados muy distantes a su área de cultivo, también se usa grandemente como sombra de café y cacao. Así sabemos que se ha introducido en la Península de Yucatán, y también en Nicaragua donde se le conoce como "guava extranjera," y muy probablemente en Costa Rica.

*Material representativo.* MEXICO. CHIAPAS: *Martínez S. et al. 20718* (MEXU). GUERRERO: *González L. & Castañeda 143* (MEXU). OAXACA: *Téllez V. 379* (MEXU). PUEBLA: *Basurto & Durán 582* (MEXU). QUINTANA ROO: *Flores 10177* (XAL). TABASCO: *Cowan 1991* (MEXU). VERACRUZ: *Ibarra M. 2156* (MEXU). GUATEMALA. EL PETEN: *Aguilar 377* (MO). EL PROGRESO: *Steyermark 43746* (F). GUATEMALA: *Harmon 2011* (GH). IZABAL: *Tún Ortíz 2436* (MO). QUEZALTENANGO: *Steyermark 33398* (F). QUICHE: *Heyde & Lux 3309* (US). SANTA ROSA: *Heyde & Lux 3280* (US). HONDURAS. ATLANTIDA: *MacQueen 35* (MEXU). COMAYAGUA: *Standley & Chacón P. 6664* (F). EL PARAISO: *L. O. Williams & Molina R. 9032* (GH). LEMPIRA: *Hughes & Chamberlain 1429* (MEXU). MORAZAN: *Molina R. 10623* (F). OCOTEPEQUE: *Molina R. 24156* (F). OLANCHO: *Ortega V. 314* (MO). EL SALVADOR. SAN SALVADOR: *Standley 21756* (GH). SANTA ANA: *Allen & Armour 6815* (F). NICARAGUA. LEON: *Grijalva et al. 4184* (MO). MANAGUA: *Araquistain 3522* (MO). MATAGALPA: *Sousa et al. 12944* (MEXU). ZELAYA: *Laguna 145* (MO). COSTA RICA. ALAJUELA: *Smith 6490* (GH). CARTAGO: *R. Torres 97* (F). HEREDIA: *Hammel 11571* (MO). LIMON: *Pennington & Zamora 13344* (K). SAN JOSE: *Zamora 1481* (MO).

**Inga pauciflora** Duchass. et Walp., Linnaea 23: 746. 1850. TIPO: Panamá: *Duchassaing s.n.* (holotipo, B; isotipo, GH).

*Inga pauciflora* Duchass. et Walp., endémica de Panamá, está muy estrechamente relacionada a *I. meissneriana* Miq. de las Guayanas y noreste de Brasil; en fruto no es posible diferenciarlas y en flor son similares, excepto que la flor de *I. pauciflora* es totalmente sésil mientras que en *I. meissneriana* las flores proximales muestran pedicelos. Afortunadamente *I. meissneriana* fue publicada un año después que *I. pauciflora*, por lo que dejamos pendiente la decisión de unirlas.

*Material representativo.* PANAMA. CHIRIQUI: *Croat 26800* (MO). DARIEN: *Stern et al. 968* (MO). VERAGUAS: *Allen 4417* (MO). ZONA DEL CANAL: *Croat 8756* (MO).

**Inga pavoniana** Don, Gen. Hist. 2: 388. 1832. TIPO: Perú: *Ruíz & Pavón s.n.* (holotipo, OXF herb Lamb.).

*Inga lindeniana* Benth., London J. Bot. 4: 608. 1845. TIPO: México. Tabasco: *Linden 726* (holotipo, K; isotipos, G (2 ej.)).

*Inga donaeana* J. F. Macbr., Field Mus. Nat. Hist., Bot. Ser. 13: 22. 1943. TIPO: Perú. San Martín: Tarapoto, *Spruce 4503* (holotipo, K; isotipos, NY, OXF).

Para demás sinónimos véase León (1966) bajo *Inga sapindoides* Willd.

Usamos el nombre de G. Don en vez de *Inga sapindoides* Willd., que fue él que escogió León (1966), ya que *I. sapindoides* se basa en un ejemplar estéril y fragmentado de Venezuela (*Bredemeyer 4*, microficha IDC. 7440. 19024 MO ex B-W) que no muestra ni la inserción de la hoja con el tallo ni las estípulas. Además, en la descripción de Willdenow (Sp. Pl. ed. 4, 4: 1012. 1806), la corola es blanca y glabra, mientras que, en la especie generalmente referida como *I. sapindoides*, la corola es verde pálido y canescente vellosa, siendo blancos los estambre. Bentham (1875) ya había discutido este problema agregando que Willdenow nunca vio las flores, sino que Bredemeyer le dio el dato. Por lo anterior empleamos a *I. pavoniana* Don, basada en un ejemplar en flor del herb. Lambert, colectado por Ruíz y Pavón, del cual no hay duda de su identidad, y dejamos a *I. sapindoides* como un nombre de aplicación dudosa.

*Material representativo.* MEXICO. CHIAPAS: *Sousa et al. 12888* (MEXU). GUERRERO: *Soto N. 7897* (MEXU). OAXACA: *Torres C. 9441* (MEXU). PUEBLA: *Basurto & Durán 400* (MEXU). TABASCO: *Sousa et al. 11740* (MEXU). VERACRUZ: *Wendt 3254* (MEXU). BELICE. EL CAYO: *Gentle 8663* (LL). STANN CREEK: *Dwyer et al. 557* (MO). TOLEDO: *Davidse & Brant 32424* (MO). GUATEMALA. ALTA VERAPAZ: *Contreras 4650* (MEXU). EL PETEN: *Contreras 3457* (MO). QUEZALTENANGO: *Croat & Hannon 63393* (MO). RETALHULER: *MacQueen & Hughes 15* (MEXU). SAN MARCOS: *Dwyer 15234* (MO). SANTA ROSA: *Heyde & Lux 6095* (MO). HONDURAS. ATLANTIDA: *Guevara 155* (MO). COLON: *Saunders 1062* (MO). CORTES: *C. Nelson et al. 2864* (MO). CHOLUTECA: *E. Repulski 74-15* (TEFH). LEPIRA: *Hughes & Chamberlain 1430* (MEXU). MORAZAN: *Molina R. 18390* (GH). OLANCHO: *Blackmore & Heath 2069* (BM). EL SALVADOR. SANTA ANA: *Villacorta & S. Martínez 275* (K). SONSONATE: *Standley 21803* (GH). NICARAGUA. CHINANDEGA: *Grijalva & Grijalva 1466* (MO). CHONTALES: *Nee 28316* (MO). GRANADA: *Moreno 4088* (MO). JINOTEGA: *Araquistain & Castro 1939* (MO). MANAGUA: *Stevens 4534* (MO). MATAGALPA: *Moreno 23594* (MO). NUEVA SEGOVIA: *Atwood et al. 6864* (MO). RIO SAN JUAN: *Araquistain 3255* (MO). ZELAYA: *Pipoly 4476* (MO). COSTA RICA. ALAJUELA: *Utley*

*& Utley 3986* (MO). CARTAGO: *Davidse & Pohl 1493* (MO). HEREDIA: *Neill 5117* (MO). LIMON: *Herrera & Martínez 2229* (MO). PUNTARENAS: *Liesner 1939* (MO). PANAMA. BOCAS DEL TORO: *von Wedel 672* (MO). CHIRIQUI: *Liesner 447* (MO). DARIEN: *Hammel 1326* (MO). PANAMA: *Croat 34431* (MO). SAN BLAS: *Elias 1790* (MO). VERAGUAS: *Nee 9837* (MO). ZONA DEL CANAL: *Croat 13491* (MO). TOBAGO: *Broadway 4355* (F). TRINIDAD: *J. D. Donnell Smith 845* (F). COLOMBIA. ANTIOQUIA: *Brand & Cogollo 87* (MO). NARIÑO: *H. León et al. 1423* (K). VALLE: *Gentry et al. 53376* (MO). VENEZUELA. ANZOATEGUI: *Steyermark 61214* (MO). MIRANDA: *Steyermark & Davidse 116212* (MO). ZULIA: *Steyermark et al. 122732* (MO). ECUADOR. NAPO: *Hurtado & Alvarado 249* (MO). PERU. SAN MARTIN: *Spruce 4503* (OXF). BOLIVIA. BENI: *T. D. Pennington et al. 13493* (K). CHILE. TARAPACA: *R. S. Shepard 300* (GH).

**Inga pezizifera** Benth., London J. Bot. 4: 587. 1845. TIPO: Guyana: *Schomburgk 124* (holotipo, K; isotipo, BM).

*Inga microstachya* Britton et Killip, Ann. New York Acad. Sci. 35: 115. 1936. TIPO: Colombia: *Mutis 3633* (holotipo, US; isotipos, G, K).

Especie cercanamente relacionada a *Inga riopalenquensis* A. H. Gentry (véase ésta), de la cual difiere tanto en caracteres florales como del fruto; ambas especies tienen una distribución que en gran medida se sobrepone.

*Material representativo.* COSTA RICA. LIMON: *Chacón 292* (MO). PANAMA. BOCAS DEL TORO: *Gordon 8* (MO). COCLE: *Knapp 3732* (MO). COLON: *Folsom 3675* (MO). ZONA DEL CANAL: *Schmalzel 585* (MO). COLOMBIA. ANTIOQUIA: *Soejarto 2912* (MO). CHOCO: *León 514* (MO). VENEZUELA. AMAZONAS: *Wurdack & Adderley 43298* (US). DELTA AMACURO: *Marcano-Berti 272* (NY). YARACUY: *Steyermark et al. 106750* (MO). GUYANA: *Forest Dept. British Guiana 3439* (NY). SURINAME: *Stahel 230* (MO). GUAYANA FRANCESA: *de Granville B5330* (MO). ECUADOR. ESMERALDAS: *Little & Dixon 21080* (US). BRASIL. (NORTE) AMAZONIA: *Ducke 1249* (MO). PARA: *Ducke 16709* (US). RORAIMA: *Prance et al. 10195* (MO).

**Inga pinetorum** Pittier, Contr. U.S. Natl. Herb. 18: 185, pl. 90. 1916. TIPO: Belice: *Peck 343* (holotipo, GH; isotipo, K).

Esta especie sería de esperarse que estuviera también en el norte de Guatemala, pero a pesar de las múltiples colectas que se han hecho de esta región, aún no hay representación de *Inga pinetorum*.

*Material representativo.* MEXICO. CHIAPAS: *Ramamoorthy 2439* (MEXU). OAXACA: *Chavelas P. & Pérez J. 70* (MEXU). TABASCO: *Téllez V. & Martínez S. 910* (MEXU). VERACRUZ: *Miller & Tenorio 713* (MO). BELICE. AUGUSTINE: *Hunt 431* (MO). EL CAYO: *Dwyer 11649* (MO). STANN CREEK: *Proctor 36217* (GH). TOLEDO: *Gentle 4149* (A).

**Inga polita** Killip, Ann. New York Acad. Sci. 35: 192. 1936. TIPO: Colombia: *Lehmann 3824* (holotipo, K). Figura 6.

Esta especie muestra claras relaciones con el complejo de *Inga umbellifera*, de la cual difiere por los pedúnculos cortos, por las brácteas florales hasta 9 mm de largo, las cuales cubren totalmente a los botones florales, y por las hojas fundamentalmente 2-folioladas.

*Inga polita* varía en sus extremos de distribución; así en Costa Rica, en el Golfo Dulce, sus hojas en la misma rama van de 2–4-folioladas mientras que, en Colombia, los folíolos son de mayor tamaño que el material mesoamericano.

*Material representativo.* COSTA RICA. PUNTARENAS: *Jiménez & Poveda 446* (MO). PANAMA. COCLE: *Davidse & Hamilton 23683* (MO). PANAMA: *McPherson 11895* (MO). SAN BLAS: *de Nevers 4651* (MO). COLOMBIA. BOLIVAR: *Gentry & Cuadros 57430* (MO). CAUCA: *Monsalve B. 1652* (MO). VALLE: *Cuatrecasas 16574* (F).

**Inga portobellensis** Beurling, Kongl. Vetensk. Acad. Handl. 1854. 122. 1856. TIPO: Panamá: *Billberg s.n.* (holotipo, S).

Especie endémica al área más húmeda de Panamá, en los alrededores de Portobelo en la provincia de Colón y norte de la Zona del Canal.

Pittier (1916) interpretó a esta especie con material de Golfo Dulce, en Costa Rica; Schery (1950) y León (1966) la han aceptado, aunque con dudas, ya que la descripción de Beurling (1856) no concuerda bien con el material de Costa Rica. Las diferencias entre ambas especies no sólo radican en el tamaño de la flor, sino también en la forma del cáliz y pelosidad de la corola (véase *I. bella* M. Sousa).

*Material representativo.* PANAMA. COLON: *Knapp & Schmalzel 3591* (MO). ZONA DEL CANAL: *Gentry 3565* (MO).

**Inga pseudoinvolucrata** M. Sousa, sp. nov. TIPO: Panamá. Panamá: Gorgas Memorial Labs yellow fever research camp, "Campamento Quatro," 5–10 km NE of Altos de Pacora, ca. 600 m, on ridge top, 21–24 Nov. 1974, *S. Mori & J. Kallunki 3406* (holotipo, MO).

Arbores e mediano procerae; rami juveniles ferrugineohirsuti. Folia 3–5-jugata; stipulae 4–5 mm longae, triangulares; foliola lanceolato-elliptica, ex ovata tenuiter obovata, apice acuminata; rhachis foliaris alata, glandulis ex subsessilibus longe stipitatis, claviformibus. Inflorescentiae capituliformes, solitariae; bracteae oblanceolatae, florum peripheric orum interdum in pseudoinvolucrum coaduna-

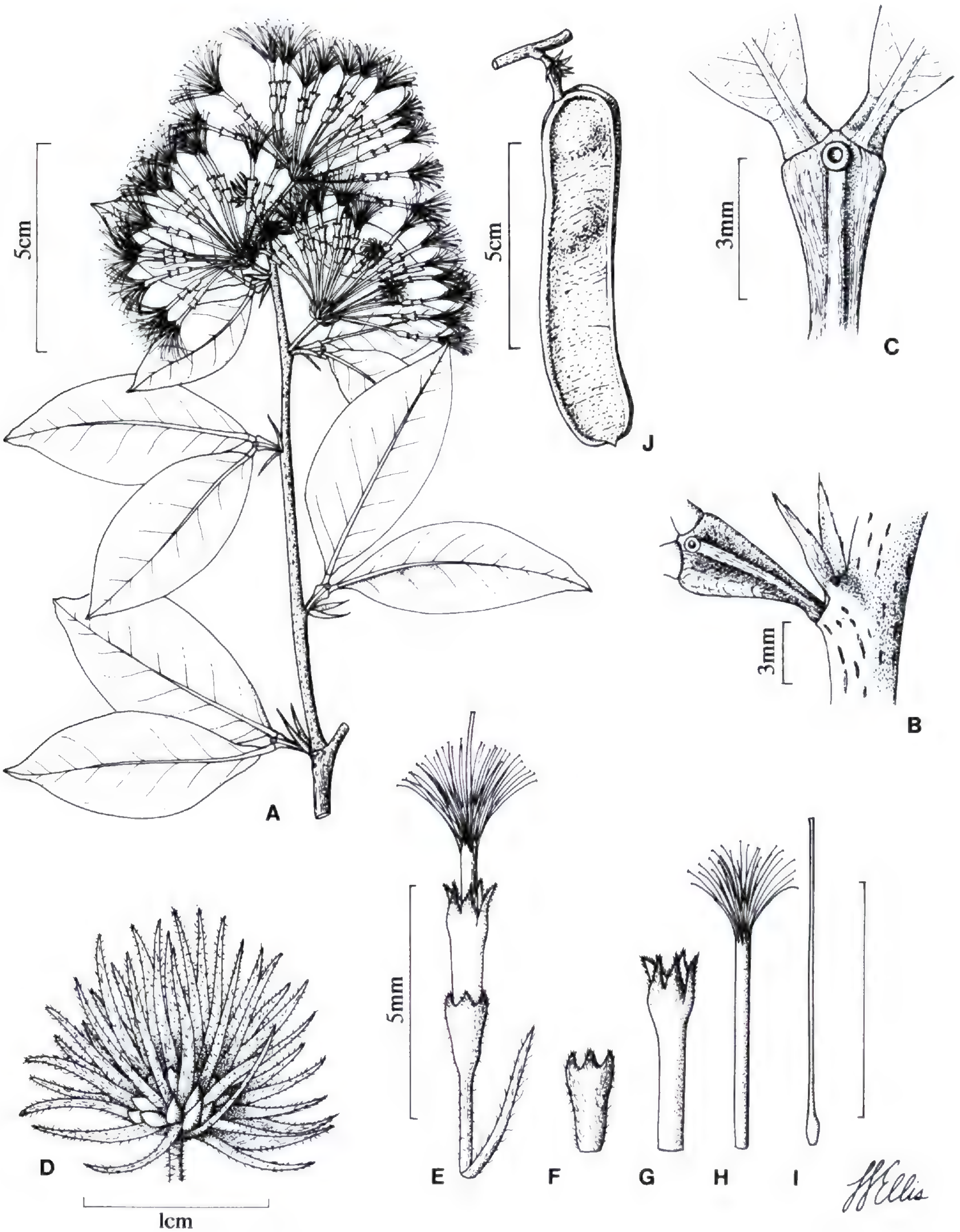


FIGURA 6. *Inga polita* Killip.—A. Rama con inflorescencia.—B. Detalle de estípulas.—C. Glándula interfoliolar. (Tomado de *McPherson 11915.*)—D. Inflorescencia en botón. (Tomado de *G. de Nevers et al. 7062.*)—E. Flor.—F. Cáliz.—G. Corola.—H. Tubo estaminal.—I. Gineceo.—J. Legumbre. (Tomado de *G. Mori et al. 6360.*)

tae; calyx tubulosus paullo inflatus, striatus, glaber; corolla tubuloso-infundibuliformis, fere glabra; tubus stamineus insertus. Legumen 18–21 cm longum, 1.8–2 cm latum, lineari-oblongum, complanatum, hirsutum, valvari-nervatum.

Arboles 5–7(–18) m; ramas teretes, tomentosas a hirsútulas con tricomas pardo-amarillentos, cuando jóvenes, posteriormente glabrescentes. Hojas 6–10-folioladas; estípulas 2–7 mm, liguladas, estria-

das, persistentes; pecíolo 0.5–1.2 cm, marginado a angostamente alado; folíolos discoloros, cartáceos, la base en ocasiones asimétrica, cuneada, rara vez obtusa, el ápice acuminado-mucronato, el haz opaco, glabro excepto seríceo a tomentoso con tricomas pardo-amarillentos sobre las nervaduras y los márgenes, el envés pálido, esparcidamente tomentoso a hirsútulo, la nervadura primaria eglandular; par basal de folíolos 2.5–3.5 × 1.5–2.2 cm, lanceolados a ovados, el par apical 4.5–7 × 2.2–3.5 cm, lanceolados elípticos en ocasiones obovados; raquis foliar 4–8 cm, alado, el ala 3–5 mm de ancho, angostamente elíptica; glándulas interfoliolares subsésiles a largamente estipitadas, clavuliformes, el cuerpo glandular 0.3–1 × 0.3–1 mm; apéndice 4–8 mm, setiforme, pronto caduco. Inflorescencia capituliforme, solitaria; pedúnculo 2–3 cm, aplanado, sulcado, hirsútulo; raquis floral muy reducido, las brácteas algo heteromorfas, las de la periferia 3 mm, frecuentemente uniéndose y formando un seudoinvolucro, cordatas a oblanceoladas, las centrales 3–4 mm, lanceoladas a oblanceoladas, persistentes. Flores sésiles o casi sésiles; botones florales con el cáliz cubriendo, se desconocen; cáliz 5–7 mm, tubular, algo inflado, estriado, glabro, sin escotaduras, los lóbulos 1–1.5 mm triangulares; corola 16–18 mm, tubular, blanca, glabra excepto pilosa con tricomas pardo-amarillentos sobre los lóbulos; tubo estaminal inserto a cortamente exerto, blanco. Legumbre 17.5–21 × 1.8–2 × 0.3 cm, más o menos aplanada a ligeramente túrgida, derecha, linear, brevistipitada en la base, rostrada en el ápice, híspida con tricomas pardo-amarillentos, las valvas inconspicuamente nervadas transversalmente, las suturas marginadas, los márgenes de las suturas aplanados.

*Distribución y hábitat.* Sólo conocida de dos áreas en los alrededores de El Llano en la Prov. Panamá, Panamá, y en el Bajo Calima en Valle, Colombia. En selvas húmedas asociada a *Catoblastus* y *Hedyosmum scaberrimum*. En altitudes entre los 100 a 600 m. Florece de finales de septiembre a noviembre (con flores marchitas en marzo) y fructifica a partir de finales de marzo.

*Paratipos.* PANAMA. PANAMÁ: along El Llano–Cartí Tupile road, 12 mi. above Pan-American Hwy., *R. L. Liesner 1177* (MO, TEX, US, WIS); EL Llano–Cartí road, km 19.1, 9°19′N, 78°15′W, *G. de Nevers & H. Herrera 5134* (MO). COLOMBIA. VALLE: Bajo Calima, Concesión Pulpapel/Buenaventura, 3°55′N, 77°W, *M. Monsalve B. 1827* (MEXU, MO).

Especie relacionada al grupo de *Ingae* con flores glabrescentes en las cuales el cáliz es amplio (inflado) y no se aplica a la corola como en *Inga bella*, *I. cordistipula*, *I. portobellensis*, e *I. spiralis*; además, es muy interesante por la combinación de caracteres tales como, glándulas interfoliolares variando de subsésiles a largamente estipitadas y clavuliformes con las inflorescencias capituliformes, combinación que sólo conocemos en *Inga saffordiana* Pittier, de la cual difiere grandemente. Un carácter muy distintivo de la nueva especie es su tendencia a formar un involucro incompleto en la periferia de capítulo y de cual toma su nombre específico.

**Inga punctata** Willd., Sp. Pl. ed. 4, 4: 1016. 1806. TIPO: Venezuela: *Bredemeyer 7* (holotipo, B-W, foto MO).

*Inga leptoloba* Schldl., Linnaea 12: 560. 1838. TIPO: México. Veracruz: *Schiede s.n.* (isotipos, BM, F, G, GH).

Para demás sinónimos véanse Schery (1950) y León (1966).

Con *Inga punctata* Willdenow creó un nuevo nombre para *Mimosa fagifolia* sensu Jacq. (Select. Stirp. Amer. Hist. 264, t. 164. 1763) non L. (Sp. Pl. 516. 1753); sin embargo, Jacquin claramente, en su publicación, se refiere a la *M. fagifolia* de Linneo (que corresponde a *Inga laurina* (Sw.) Willd.; véase ésta), además de que todos los demás elementos concuerdan con ella. Por lo anterior, Willdenow interpretó la descripción y lámina de Jacquin como otra especie de la cual él tenía un ejemplar de Caracas, Venezuela, con la que basó su descripción. *Inga punctata* Willd. está basada en elementos heterogéneos, de los cuales, afortunadamente los subsecuentes autores a partir de DeCandolle (Prodr. 2: 435. 1825) han interpretado la especie con el material de Venezuela y no con él de La Martinica. Así *Mimosa fagifolia* en la obra de Jacquin no debe ser interpretada como un homónimo tardío, y por tanto no se trata de un nombre ilegítimo.

El concepto de esta especie para Mesoamérica, fue muy bien interpretado, por Schery (1950) y León (1966); sin embargo, debido a sus similitudes, pero discernibles diferencias con *Inga latipes* Pittier (véase ésta y discusión de León, 1966) e *I. leiocalycina* Benth. (véase ésta y discusión de Poncy, 1985) se les ha querido incluir como extremos de variación de *I. punctata*. En Sudamérica el problema es más complejo; así tenemos a *I. strigillosa* Spruce ex Benth., la cual Poncy (1985) sugiere que con más información debería ser sinonimizada con *I. punctata* pero, por lo pronto la coloca de sinónimo de *I. leiocalycina* Benth., tanto el tipo (*Spruce 1755*, BM, G, K (2 ej.)) como de varios ejemplares de la Amazonía (Perú. Amazonas:

*Ferreyra 5037*, MO. Bolivia. Pando: *Sperling & King 6534*, NY. Brasil (Norte). Amazonas: *Berg et al. 19714*, NY; Maranhâo: *Daly et al. D.669*, MO; Rondônia: *Prance et al. 5467*, NY). Aquí considero a *I. strigillosa* como una especie aparte, que se caracteriza por un raquis floral muy corto, paucifloro y las brácteas filiformes que sobrepasan a los botones florales, dando un aspecto de inflorescencia parecido a *Dalea*.

En cuanto a los taxa infraespecíficos descritos para *Inga punctata*, no los estamos considerando aquí. Así *I. punctata* var. *elongata* J. F. Macbr. del Ecuador y Perú (holotipo, *Killip & Smith 29406*, F), con flores cuya corola llega hasta 14 mm de largo y raquis foliar angostamente alado, debe corresponder a otra especie. Por otro lado la subespecie *chagrensis* Pittier (tipo, *W. R. Maxon 4788*; isotipo, BM) y la variedad *panamensis* Benth. (sintipos, *Sutton Hayes 357*, BM, K; *Seemann 406*, K (2 ej.)) no parecen diferentes al resto de *I. punctata*.

*Material representativo.* MEXICO. CHIAPAS: *Ton 7238* (MEXU). HIDALGO: *Tenorio 2515* (MEXU). OAXACA: *Torres C. et al. 2517* (MEXU). PUEBLA: *Basurto & Durán 555* (MEXU). TABASCO: *Sousa et al. 12792* (MEXU). VERACRUZ: *Cedillo T. 2482* (MEXU). BELICE. BELICE: *Liesner & Dwyer 1487* (MO). EL CAYO: *Dwyer 12724* (MO). STANN CREEK: *Dwyer et al. 463* (MO). TOLEDO: *Whitefoord 3191* (BM). GUATEMALA. ALTA VERAPAZ: *Contreras 7868* (LL). IZABAL: *Contreras 9234* (LL). EL PETEN: *Lundell 18335* (MEXU). RETALHULEU: *Hughes et al. 1383* (MEXU). SAN MARCOS: *White 5274* (MO). SANTA ROSA: *Téllez V. 619* (MEXU). HONDURAS. ATLANTIDA: *Standley 58670* (A). COLON: *Saunders 598* (MO). COMAYAGUA: *Edwards P-436* (A). COPAN: *Blackmore & Chorley 3796* (BM). CORTES: *Pennington 13394* (K). EL PARAISO: *Molina R. & Molina 27906* (F). MORAZAN: *Tucker 761* (LL). MOSQUITIA: *Gentry et al. 7508* (MO). OLANCHO: *Croat et al. 64451* (MO). EL SALVADOR. COMASAGUA: *Calderón 1354* (GH). LA LIBERTAD: *Rohweder 2943* (MO). SANTA ANA: *Villacorta & S. Martínez 273* (K). NICARAGUA. BOACO: *Stevens 14568* (MO). CHONTALES: *Nee 28346* (MO). JINOTEGA: *Vega & Quezada 188* (MO). MATAGALPA: *Sousa et al. 12925* (MEXU). NUEVA SEGOVIA: *Moreno et al. 24765* (MO). RIVAS: *Sandino 938* (MO). ZELAYA: *Stevens 7221* (MO). COSTA RICA. ALAJUELA: *Taylor 3718* (MO). GUANACASTE: *Sousa et al. 12753* (MEXU). HEREDIA: *D. Smith 1187* (MO). LIMON: *Stevens et al. 25105* (MO). PUNTARENAS: *Burger et al. 10573* (F). SAN JOSE: *Tonduz 7020* (MO). PANAMA. BOCAS DEL TORO: *McPherson 11627* (MO). COCLE: *Allen 3700* (MO). COLON: *Hamilton & Stockwell 3699* (MO). CHIRIQUI: *Hampshire & Whitefoord 743* (BM). DARIEN: *Stern et al. 548* (MO). LOS SANTOS: *McPherson 13507* (MO). PANAMA: *Tyson 6745* (MO). SAN BLAS: *Gentry 6412* (MO). VERAGUAS: *Antonio 2404* (MO). ZONA DEL CANAL: *Croat 6248* (MO). TOBAGO: *Broadway 3909* (F). COLOMBIA. ANTIOQUIA: *Rentería et al. 1640* (MO). CHOCO: *von Sneidern 4879* (MO). SANTANDER: *Gentry & Forero 15487* (MO); VALLE: *Devia 260* (MO). VENEZUELA. MIRANDA: *Croat 21768* (MO). TACHIRA: *Steyermark et al. 120093* (MO). TRUJILLO: *Benítez de Rojas 1879* (MO). YARACUY: *Rutkis 470* (MO). ECUADOR. NAPO: *Cerón M. 1358* (MO). PERU. CUZCO: *Vargas C. 7318* (MO). BOLIVIA. SANTA CRUZ: *Steinbach 7396* (MO).

**Inga quaternata** Poeppig, Nov. Gen. Sp. Pl. 3: 79. 1845. TIPO: Brasil: *Poeppig 121* (holotipo, W; isotipo, F).

Para sinónimos véase León (1966).

Especie muy variable que León (1966) caracterizó muy bien y seguimos su concepto. Sólo agregamos que en su extremo norte en Veracruz, México, la inflorescencia en ocasiones pasa de capituliforme a una espiga corta corimbosa, dandole aspecto de *Inga nobilis* Willd.

*Material representativo.* MEXICO. CHIAPAS: *Meave et al. B-651* (MEXU). VERACRUZ: *Sinaca C. 992* (MEXU). BELICE. STANN CREEK: *Gentry 7895* (MO). TOLEDO: *Dwyer 11168* (MO). GUATEMALA. EL PETEN: *Contreras 6209* (MEXU). IZABAL: *Marshall et al. 329* (NY). HONDURAS. ATLANTIDA: *Yuncker et al. 8337* (BM). COPAN: *Molina R. 11758* (F). CORTES: *Nelson et al. 3072* (MO). NICARAGUA. RIO SAN JUAN: *Moreno 23265* (MO). ZELAYA: *Ortíz 154* (MO). COSTA RICA. ALAJUELA: *Liesner & Judziewicz 14904* (WIS). CARTAGO: *Liesner & Judziewicz 14597* (MO). GUANACASTE: *Haber & Bello 2668* (MO). LIMON: *Gómez P. 24115* (MO). PUNTARENAS: *Jiménez 683* (MO). PANAMA. BOCAS DEL TORO: *Cooper & Slater 13* (F). COLON: *Knapp 1326* (MO). CHIRIQUI: *Pittier 5270* (US). DARIEN: *Stern et al. 238* (MO). HERRERA: *McPherson 10325* (MO). PANAMA: *Duke 5890* (MO). SAN BLAS: *Dwyer 6844* (MO). ZONA DEL CANAL: *Croat 12598* (MO). PUERTO RICO: *Little 13699* (F). COLOMBIA. EL META: *Killip 34459* (MO). SANTANDER: *Killip & Smith 15477* (US). VENEZUELA. ARAGUA: *Pittier 14140* (US). MERIDA: *Breteler 4173* (MO). MIRANDA: *Pittier 6012* (US). ECUADOR. MORONA SANTIAGO: *Cerón et al. 486* (MO). NAPO: *Neill & Manning 7992* (MO). PASTAZA: *MacBryde 1517* (MO). PERU. AMAZONAS: *Wurdack 2217* (MO). CUZCO: *Wasshausen & Encarnación 753* (MO). LORETO: *Croat 19389* (MO). MADRE DE DIOS: *Barbour 5737* (MO). UCAYALI: *Gentry & Díaz 58596* (MO). BOLIVIA. BENI: *Rusby 990* (MO). BRASIL. (NORTE) AMAZONIA: *Cid & Souza 3005* (MO).

**Inga riopalenquensis** A. H. Gentry, Selbyana 2: 39, pl. 12A. 1977. TIPO: Ecuador: *Dodson 5463* (holotipo, MO; isotipo, US).

Especie cercana a *Inga pezizifera* Benth., de la cual difiere fundamentalmente por el tan particular fruto leñoso con proyecciones en las valvas, la pelosidad de la corola, y el cáliz de mayor tamaño. En el material de Costa Rica, sus legumbres son más verrugosas que las de Ecuador.

Aquí se da una nueva distribución a una especie descrita recientemente como endémica del Chocó ecuatoriano (Río Palenque). Gentry (1982) tabula las relaciones fitogeográficas de Río Palenque con Mesoamérica y encuentra que el 18% de las es-

pecies tienen el patron de "América Central a Ecuador occidental (sin incluir el Amazonía)," lo que representa una alta proporción de una área que él considera natural.

*Material representativo.* COSTA RICA. HEREDIA: *Hartshorn 1842* (MO). PUNTARENAS: *Utley & Utley 4867* (MO). COLOMBIA. BOYACA: *Lawrance 783* (MO). ECUADOR. LOS RIOS: *Gentry 31009* (MO)

**Inga rubiginosa** (Rich.) DC., Prodr. 2: 434. 1825. Basiónimo: *Mimosa rubiginosa* Rich., Actes Soc. Hist. Nat. Paris 1: 113. 1792. TIPO: Guayana Francesa: *Leblond s.n.* (holotipo, G-DEL, foto TEX).

*Inga standleyana* Pittier, Contr. U.S. Natl. Herb. 18: 204. 1916. TIPO: Panamá: *Pittier 5496* (holotipo, US; isotipo, US).

Dentro de la variabilidad de *Inga rubiginosa*, *I. standleyana* Pittier parece representar un extremo con flores más robustas y en general un poco más cortas, con distribución en Panamá a Venezuela, mientras que *I. rubiginosa* sensu stricto es de las Guayanas y norte de Brasil. Sin embargo, a diferencia de León (1966), las unimos en base a su débil diferencia, proponiendo que posteriormente podría formalizarse a nivel infraespecífico.

*Material representativo.* PANAMA. DARIEN: *Pittier 5496* (US). COLOMBIA. ANTIOQUIA: *Brant & Escobar 1275* (MEXU). VENEZUELA. BOLIVAR: *Blanco 450* (NY). DELTA AMACURO: *Wurdack & Monachino 39650* (NY). MERIDA: *Breteler 5034* (U). GUYANA: *A. C. Smith 2909* (MO). SURINAME: *B. W. [Sur. For. Dept.] 6074* (MO). GUAYANA FRANCESA: *Sastre 6121* (MO). BRASIL. (NORTE) AMAPA: *Pires et al. 50274* (MO). PARA: *Maciel et al. 468* (TEX). (NORESTE) MARANHAO: *Fróes 1749* (MO).

**Inga ruiziana** Don, Gen. Hist. 2: 391. 1832. TIPO: Perú: *Ruíz & Pavón s.n.* (lectotipo, designado aquí, OXF herb. Lamb., con hoja y flores; isolectotipos, BM, OXF).

*Inga fagifolia* Don, Gen. Hist. 2: 391. 1832. TIPO: Perú: *Ruíz & Pavón s.n.* (holotipo, OXF).

Para demás sinónimos véase Schery (1950).

León (1966: 301) cita como tipo de *Inga ruiziana* Don a *Ruíz 5*, de la cual he visto un ejemplar en el Smithsonian (US); por otro lado Macbride (1943: 40) citó como tipo una colecta de Ruíz y Pavón, sin informar sobre el herbario ni alguna colecta determinada. Sin embargo, el material que George Don vió y citó en la descripción original fue el del Herbario de H. B. Lambert que fue comprado por Fielding, ahora Herbario Fielding en la Universidad de Oxford, donde existen tres ejemplares de *I. ruiziana* colectados por Ruíz y Pavón: uno está anotado como "*Mimosa fagifolia* sp. nov. del Perú" (se trata del tipo de *I. fagifolia* Don) y los otros dos como "*Mimosa* sp. nov. del Perú." De estas dos se escogió el ejemplar con hoja y flores como lectotipo.

Especie poco variable de la Amazonía que llega hasta las selvas de la vertiente Caribe de Nicaragua.

*Material representativo.* NICARAGUA. CHONTALES: *Stevens 2842* (MO). JINOTEGA: *Moreno 946* (MO). MATAGALPA: *Araquistain & Moreno 2700* (MO). RIO SAN JUAN: *Stevens 4917* (MO). ZELAYA: *Vincelli 368* (MO). COSTA RICA. ALAJUELA: *Herrera 1844* (MO). CARTAGO: *Tonduz 13054* (GH). HEREDIA: *Schatz & Bockbrader 1042* (MO). LIMON: *Pittier 16646* (US). PUNTARENAS: *Janzen 10454* (MO). SAN JOSE: *Skutch & Barrantes 5110* (GH). PANAMA. BOCAS DEL TORO: *Blum 1346* (MO). COLON: *Nee 9114* (MO). CHIRIQUI: *Liesner 456* (MO). DARIEN: *Hartman 12227* (MO). SAN BLAS: *Mori et al. 6848* (MO). ZONA DEL CANAL: *Dwyer 1455* (MO). COLOMBIA. CAUCA: *Cuatrecasas 14212* (US). CHOCO: *Duke 9892* (MO). VALLE: *Cuatrecasas 16522* (US). ECUADOR. NAPO: *Neill & Palacios 7120* (MO). PASTAZA: *Cerón et al. 4356* (MO). PERU. AMAZONAS: *Huashikat 1424* (MO). CUZCO: *Núñez 6524* (MO). HUANUCO: *Seidenschwarz 16211* (MO). LORETO: *Mexía 6176* (MO). LIMA: *Medina 142* (MO). MADRE DE DIOS: *Núñez 10592* (MO). PASCO: *Gentry et al. 63235* (MO). SAN MARTIN: *Ferreyra 7804* (MO). UCAYALI: *Begazo 23* (MO). BRASIL. (NORTE) AMAZONIA: *Riedel s.n.* (K).

**Inga saffordiana** Pittier, Contr. U.S. Natl. Herb. 18: 176. 1916. TIPO: Panamá: *Pittier 5676* (holotipo, US).

De esta notable especie de *Inga* lo que más ha llamado la atención de los botánicos es su inflorescencia caulinar, carácter que ahora sabemos se presenta en al menos cinco especies de *Inga*, tres de las cuales se encuentran en Mesoamérica. Sin embargo, el carácter de esta especie que me parece único, es su cáliz, el cual es casi totalmente partido en cinco lóbulos lanceolado-aleznados, que persisten en el fruto.

*Material representativo.* PANAMA. DARIEN: *Hammel et al. 16128* (MO). COLOMBIA. ANTIOQUIA: *Rentería et al. 3790* (MO). CHOCO: *Fernández 267* (US).

**Inga samanensis** L. Uribe, Mutisia 1: 5. 1952. TIPO: Colombia: *Uribe-Uribe 1903* (isotipo, US).

*Inga squamigera* León, Ann. Missouri Bot. Gard. 53: 306. 1966. TIPO: Costa Rica: *León 4869* (holotipo, CR).

*Inga paludicola* A. R. Molina, Ceiba 18: 101. 1974. TIPO: Nicaragua: *Molina R. 2443* (holotipo, F).

Especie muy característica por tener legumbres con indumento escuamoso, carácter poco común en las especies mesoamericanas. El material de

Colombia no difiere del de Mesoamérica, por lo que adoptamos el nombre más antiguo de Uribe.

*Material representativo.* NICARAGUA. MATAGALPA: *Sandino 2802* (MO). ZELAYA: *Pipoly 5086* (MO). COSTA RICA. ALAJUELA: *Hartshorn 983* (F). HEREDIA: *Hammel 11050* (MO). LIMON: *Gómez P. et al. 22768* (MO). PANAMA. BOCAS DEL TORO: *Kirkbride et al. 487* (MO). COLON: *McPherson 8517* (MO). COLOMBIA. ANTIOQUIA: *Cogollo 1274* (MO).

**Inga semialata** (Vell. Conc.) C. Martius, Flora 20(2): Beibl. 111. 1837. Basiónimo: *Mimosa semialata* Vell. Conc., Fl. Flumin. 1: t. 5. 1831. TIPO: *Velloso, Fl. Flumin. 11: t. 5. 1831.* Figura 7.

*Inga marginata* Willd., nom illeg., Sp. Pl. ed. 4, 4: 1015. 1806. TIPO: Venezuela: *Bredemeyer s.n.* (holotipo, B-W, foto, MO).

*Inga tysonii* T. S. Elias, Ann. Missouri Bot. Gard. 53: 377. 1966. TIPO: Panamá: *Tyson y Blum 3803* (holotipo, MO).

Aquí estoy usando el nombre de Martius ya que él de *Inga marginata* Willd. es superfluo, porque Willdenow no había hecho el cambio que correspondía de *Mimosa fagifolia* L. (Sp. Pl. 516. 1753) a *Inga fagifolia*, sino creó un nuevo nombre que resulta ilegítimo. La descripción de *I. marginata* Willd., y el ejemplar citado (*Bredemeyer s.n.* de Caracas, Venezuela, B-W) corresponden a otra especie diferente a la de Linneo; además se cita como sinónimo a *Mimosa bourgonii* Aublet (Hist. Pl. Guiane 2: 941, t. 358. 1775), la cual corresponde a otra tercera especie. El nombre de Willdenow ha persistido en uso debido a que Bentham (1875) lo citó como, "*Inga marginata* Willd. excl. syn.," excluyendo los "sinónimos." En la lista de sinónimos de *I. marginata* desde Bentham (1875), *I. sapida* Kunth (in Humb., Bonpl. et Kunth, Nov. Gen. Sp. 6: 286. 1823) es el binomio más antiguo a escoger; sin embargo, se trata de un nombre basado en un ejemplar estéril de difícil determinación, y la descripción del fruto es muy general ("legumina qunique-aut sex pollicaria subarcuata") para permitir su identificación a nivel de especie; además como el mismo Kunth aclaró, él no vio el fruto sino la información se la proporcionó Humboldt, así *I. sapida* queda incertae sedis.

Aquí también incluyo como sinónimo a *Inga tysonii* T. S. Elias, la cual parece no sostenerse como especie aparte debido a la gran variabilidad de *I. semialata*. Los caracteres diagnósticos usados por Elias (1966) son la inflorescencia congesta y el pedúnculo corto.

Respecto a la gran variación de esta especie es necesario apuntar que la población del Cerro Jefe, en Panamá, entre los 800 a 1,800 m de altitud ha sido identificada como *Inga fagifolia* (L.) Willd. ex Benth. [*I. laurina* (Sw.) Willd.], debido quizá a que sus raquis foliares son teretes a submarginados. Lo interesante de esta población del Cerro Jefe es que fácilmente se diferencia de las del resto de Mesoamérica: así de ellas difiere por tener estípulas más cortas, el raquis foliar terete a submarginado, las láminas foliares coriáceas, la corola más larga, esparcidamente serícea, y el fruto más ancho con las valvas verrugoso-lenticeladas; pero si se revisa el material de esta extensa especie se ve que en Sudamérica cada uno de los caracteres de la población del Cerro Jefe aparece. Así, por ejemplo, las poblaciones del Perú (*Ancuash 263*, MO) cuentan con los frutos tan o más anchos. Por estas razones parece que la llegada de *I. semialata* a Mesoamérica ocurrió al menos en dos ocasiones y que la población de Cerro Jefe es una muestra de caracteres diferentes a la de las áreas más bajas de Costa Rica y Panamá.

En el límite norte de esta especie (Chiapas y Veracruz), existen otras poblaciones que muestran el raquis foliar terete a submarginado, pero con otras combinaciones de caracteres a las de Cerro Jefe, incluyendo: folíolos de mayor tamaño, cartáceos a subcoriáceos, y un fruto grande, pero con las valvas aplanadas; este último carácter no ha sido reportado para la especie. Esta última variante aparentemente (desconocemos el fruto) está también representada en Costa Rica (Cartago, *Lent 1122*, GH; Guanacaste, *Herrera 753*, MO) y Panamá (Chiriquí, *McPherson 9886*, MO), pero es más escasa que la forma de raquis foliar alado.

La ilustración que aquí se muestra (Fig. 7) corresponde a la población del Cerro Jefe.

*Material representativo.* MEXICO. CHIAPAS: *Ton 4947* (MEXU). VERACRUZ: *Sinaca C. 1024* (MEXU). COSTA RICA. ALAJUELA: *Haber et al. 1817* (MO). CARTAGO: *Utley & Utley 5063* (MO). GUANACASTE: *Herrera 753* (MO). HEREDIA: *D. Smith 354* (MO). LIMON: *Grayum et al. 4327* (MO). PUNTARENAS: *O. Jiménez & R. Zúñiga 766* (MO). SAN JOSE: *Skutch 4288* (GH). PANAMA. BOCAS DEL TORO: *von Wedel 1807* (MO). COCLE: *Hammel 2651* (MO). COLON: *Nee 9078* (MO). CHIRIQUI: *Croat 22570* (MO). DARIEN: *McPherson 12257* (MO). LOS SANTOS: *McPherson 9244* (MO). VERAGUAS: *Croat 34174* (MO). ZONA DEL CANAL: *Blum & Tyson 1997* (MO). COLOMBIA. AMAZONAS: *Galeano et al. 1009* (MO). ATLANTICO: *Romero C. 4075* (MO). CHOCO: *Gentry & Fallen 17744* (MO). VENEZUELA. LARA: *Steyermark & Carreño E. 107587* (MO). ZULIA: *Bunting 11986* (MO). GUYANA: *Tutin 460* (US). SURINAME: *B. W. (Sur. For. Dept.) 3223* (MO). GUAYANA FRANCESA: *Sastre 6474* (MO). ECUADOR. ESMERALDAS: *Little & Dixon 21117* (MO). NAPO: *Neill & Manning 7998* (MO). PERU. AMAZONAS: *Ancuash 263* (MO). CUZCO: *C. Vargas C. 15237* (MO). LORETO: *Croat 20245* (MO). MADRE DE DIOS: *Terborgh 6206* (MO). PASCO:

FIGURA 7. *Inga semialata* (Vell Conc.) C. Martius.—A. Rama con inflorescencia. —B. Glándula interfoliolar. (Tomado de *McPherson 7443.*)—C. Botón floral y brácteas. (Tomado de *M. Correa et al 550.*)—D. Flor.—E. Cáliz.—F. Corola.—G. Tubo estaminal.—H. Gineceo. (Tomado de *McPherson 7443.*)—I. Fruto. (Tomado de *McPherson 10623.*)

*Gentry et al. 42055* (MO). PUNO: *Núñez & Muñoz 5268* (MO). SAN MARTIN: *Klug 2669* (MO). UCAYALI: *Begazo 1* (MO). BOLIVIA. LA PAZ: *Gentry & Solomon 44522* (MO). PANDO: *Sperling & King 6532* (MO). SANTA CRUZ: *Neill et al. 9292* (MO). BRASIL. (NORTE) AMAZONIA: *Krukoff 6437* (MO). PARA: *Silva & Souza 2227* (NY). RONDONIA: *Prance et al. 6050* (NY). (NORESTE) BAHIA: *Luschnath 144* (MO). (CENTRO OESTE) GOIAS: *Heringer 12222* (MO). (SUDESTE) MINAS GERAIS: *Mexía 5152* (MO). RIO DE JANEIRO: *Duarte & Pereira 4748* (MO). SAO PAULO: *Gentry & Silva 58732* (MO). (SUR) PARANA: *Hatschbach 44510* (MO). SANTA CATARINA: *Conrad & Dietrich 2098*

(MO). ARGENTINA. MISIONES: *Eskuche 379* (MO). PARAGUAY. ALTO PARANA: *Brunner et al. 895* (MO).

*Material representativo de la población de Cerro Jefe.* PANAMA. PANAMA: *Antonio 3212* (MO), *Carrasquilla 2186* (MO), *Correa A. et al. 550* (NY), *4579* (MO), *Folsom & Harp 1359* (MEXU), *2007* (MEXU), *McPherson 7443* (MO), *9796* (MO), *10632C* (MO), *12333* (MO).

**Inga sertulifera** DC., Prodr. 2: 436. 1825. TIPO: Guayana Francesa: *Stoupy s.n.* (holotipo, P-JU 14523 [IDC. microficha 6206. 1067: III. 3]).

*Mimosa coriacea* Pers., Syn. Pl. 2: 262. 1806. *Inga coriacea* (Pers.) Desv., J. Bot. Agric. 3: 71. 1814, non Humb. et Bonpl. ex Willd. 1806.

Para demás sinónimos véase Poncy (1985).

Esta especie ha sido identificada en Mesoamérica como *Inga heterophylla* Willd., y por ello no se había reportado para el área. Es una especie amazónica bastante variable cuyos límites aún no me están claros y por ello no estoy considerando las variedades descritas. En nuestra área los raquis foliares son teretes.

*Material representativo.* COSTA RICA. ALAJUELA: *Molina R. et al. 17747* (MO). GUANACASTE: *Hammel 17501* (MO). LIMON: *Davidse & Herrera 31315* (MO). PUNTARENAS: *Sánchez & Poveda 1277* (MO). PANAMA. COCLE: *Antonio 3569* (MO). DARIEN: *Gentry & Mori 14035* (MO). HERRERA: *McPherson 10934* (MO). PANAMA: *Nee et al. 8784* (MO). ZONA DEL CANAL: *Gentry 1897* (WIS). COLOMBIA. CHOCO: *Forero & Jaramillo 4333* (MO). VALLE: *Cuatrecasas 17422* (US). VENEZUELA. AMAZONAS: *Level 76* (MO). SUCRE: *Steyermark et al. 121563* (MO). GUYANA: *de la Cruz 2311* (US). SURINAM: *Amshoff 2024* (MO). GUAYANA FRANCESA: *Wachenheim 299* (MO). ECUADOR. NAPO: *Palacios 1856* (MO). PASTAZA: *Holguer 4655* (MO). PERU. AMAZONAS: *Tunqui 837* (MO). LORETO: *Rimachi Y. 7135* (MO). MADRE DE DIOS: *Núñez 5469* (MO). BOLIVIA. LA PAZ: *Krukoff 11280* (MO). BRASIL. (NORTE) AMAPA: *Irwin et al. 47498* (F). AMAZONIA: *Vieira et al. 255* (MO). PARA: *Prance et al. P25414* (MO). RONDONIA: *Nee 34810* (F). (CENTRO OESTE) MATO GROSSO: *Berg et al. P19865* (MO).

**Inga sierrae** Britton et Killip, Ann. New York Acad. Sci. 35: 123. 1936. TIPO: Colombia: *Archer 1366* (holotipo, US).

*Inga brenesii* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 495. 1937. TIPO: Costa Rica: *Brenes 5121* (holotipo, F).

Esta especie es muy característica por sus hojas cocleadas, sus ocasionales glándulas supernumerarias, y sus flores congestas en una espiga muy corta; se ubica en el complejo de *Inga villosissima* Benth., *I. tenella* M. Sousa, *I. dasycarpa* M. Sousa, e *I. leonis* Zamora. El material de Colombia y el de Mesoamérica no parecen diferir, por lo que las unimos bajo el nombre más antiguo de *I. sierrae*.

*Material representativo.* NICARAGUA. ZELAYA: *Molina R. 15086* (F). COSTA RICA. ALAJUELA: *Brenes 4988* (F). GUANACASTE: *Haber & Bello C. 2864* (MO). PUNTARENAS: *Téllez V. 4369* (MEXU). SAN JOSE: *Jiménez M. 2620* (NY). PANAMA. CHIRIQUI: *Him 297* (MO). COLOMBIA. ANTIOQUIA: *Archer 1366* (US). HUILA: *Little 9040* (NY).

**Inga sinacae** M. Sousa et Ibarra-Manríquez, sp. nov. TIPO: México. Veracruz: Estación de Biología Tropical Los Tuxtlas, Mpio. San Andrés Tuxtla, 18°34′–36′N, 95°04′–09′O, 4 mayo 1984, *G. Ibarra, B. G. Gómez V. & S. Sinaca C. 1547* (holotipo, MEXU; isotipos, MEXU, MO). Figura 8.

Arbores medianae, ramis juvenilibus brunneo-luteo-tomentosis. Folia 2–4(–5)-jugata; stipulae 2.5–4 mm longae, ovatae; foliola chartacea; rhachis foliaris ex teres anguste alata glandulis sessilibus urceolatis. Inflorescentiae racemosae; rachis floralis 2.5–5(–8) cm longa; bracteae crassae, ex ovatae suborbiculares, deciduae. Flores sessiles; alabastra floralia calice aperto; calyx tubulosus, laevis, cinereo-tomentosus; corolla tubulosa, e canescenti-villoso lanata. Legumen usque 35 cm longum, latum, incrassatum, complanatum, oblongum, brunneo-lutescenti-hirsutum.

Arboles 6–22 m; ramas teretes, tomentosas con tricomas pardo-amarillentos. Hojas 4–8(–10)-folioladas; estípulas 2.5–4 mm, ovadas, caducas; peciólo 1.5–3.5(–7) cm, terete; folíolos discoloros, cartáceos, la base de simétrica a ligeramente asimétrica, generalmente cuneada en ocasiones obtusa, el ápice obtuso a acuminado, el haz opaco, posteriormente brillante, esparcidamente canescente seríceo después glabro, el envés opaco, esparcidamente canescente velutino, las nervaduras primaria y secundarias canescentes a tomentosas con tricomas amarillo pálido, la nervadura primaria eglandular, el par basal de folíolos 6–9 × 3–4.5 cm, generalmente elípticos, en ocasiones ovados, el par apical 11–17 × 4.5–6 cm, lanceolados a elípticos; raquis foliar 4–12 cm, tomentoso con tricomas pardo-amarillentos, terete, marginado a angostamente alado principalmente entre los pares distales de folíolos, el ala hasta 6 mm de ancho, elíptica a oblanceolada; glándulas interfoliolares sésiles, urceoladas, el cuerpo glandular 0.9–1 × 0.9–1 mm; apéndice muy reducido o ausente. Inflorescencias en racimos solitarios; pedúnculo 2–4(–8) cm, terete, aparentemente liso, tomentoso con tricomas pardo-amarillentos; raquis floral 2.5–5(–8) cm, las flores esparcidas particularmente las proximales, las brácteas homomorfas 1.5–2 mm, gruesas, ligeramente cóncavas, ovadas a suborbiculares, caducas. Flores sésiles; botones florales con el cáliz abierto, obtusos; cáliz 9–13 mm, tubular, liso, cinéreo tomentoso, sin escotaduras, los lóbulos triangulares; corola 2.3–3.2 cm, tubular, blanco-

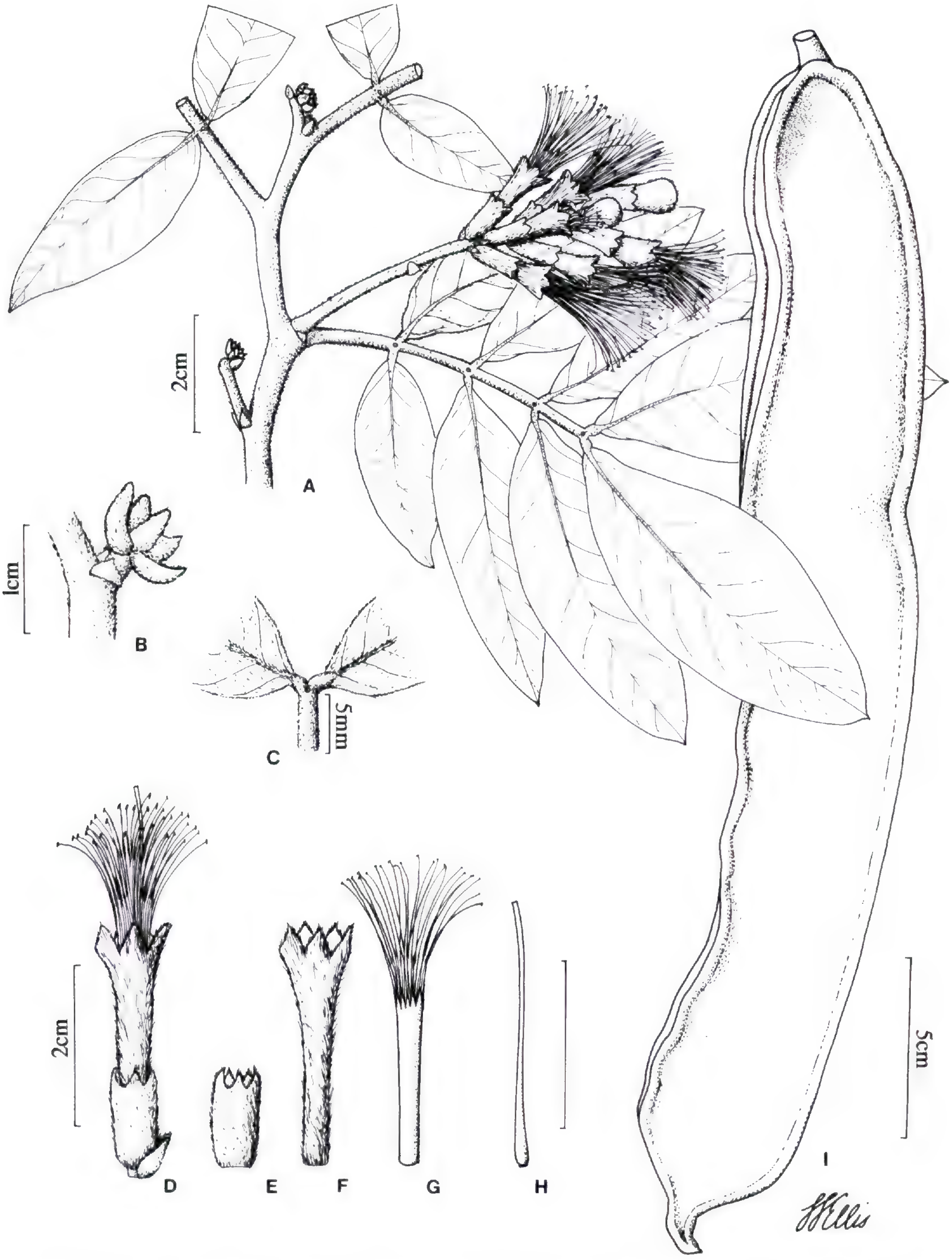


FIGURA 8. *Inga sinacae* M. Sousa et Ibarra-Manríquez.—A. Rama con inflorescencia. (Tomado de *G. Ibarra M. 1547.*)—B. Detalle de yema. (Tomado de *S. Sinaca C. 184.*)—C. Glándula interfoliolar. (Tomado de *G. Ibarra M. 1547.*)—D. Flor.—E. Cáliz.—F. Corola.—G. Tubo estaminal.—H. Gineceo. (Tomado de *R. Cedillo T. 3600.*)—I. Legumbre. (Tomado de *G. Ibarra & S. Sinaca C. 1836.*)

verdosa, densamente vellosa a lanosa con tricomas canescentes; tubo estaminal inserto, blanco, los estambres erectos en el crepúsculo. Legumbre 13–35 × (2.3–)3–5 × 0.8–1.5 cm, aplanada, derecha a curveada, oblonga, sésil en la base, apiculada a rostrada en el ápice, hirsuta con tricomas pardo-amarillentos, las valvas aplanadas, las suturas derechas, aplanadas a 1-sulcadas.

*Distribución y hábitat.* Hasta ahora sólo conocida de la región volcánica de Los Tuxtlas en el sur de Veracruz, México, en el estrato medio de selvas altas perennifolias y en encinares. En altitudes entre 200 y 650 m. Florece de abril a junio, fructifica de junio a agosto.

*Nombre vernáculo.* Vaina peluda.

*Usos.* Sombra de cafetos.

*Paratipos.* MEXICO. VERACRUZ: Mpio, Catemaco, Río Piso, a 3 km al N de La Palma, camino a Playa Escondida, *R. Cedillo T. 2761* (MEXU), *2762* (MEXU), *3600* (MEXU, MO), *3602* (MEXU, MO), *3624* (MEXU), *3626* (MEXU, MO); Mpio. San Andrés Tuxtla, Estación de Biología Tropical "Los Tuxtlas," *R. Cedillo T. 3647* (MEXU), *G. Ibarra M. 217* (MEXU), *1836* (MEXU, MO); Laguna Escondida, 3 km NO de la Estación de Biología Tropical "Los Tuxtlas," *S. Sinaca C. 184* (MEXU, MO), *893* (MEXU, MO); sin Mpio., Arriba de San Fernando, *A. Gómez-Pompa 4861* (MEXU).

*Inga sinacae* no parece tener un pariente tan cercano que permita comparación; sin embargo, tiene fuertes relaciones con la serie *Longiflorae* de Bentham. Con esta especie se ilustra muy bien lo variable del raquis foliar, el cual, aun en el mismo árbol, varía de terete a alado pasando por marginado.

Esta especie se dedica a Santiago Sinaca Colín (1959–), colector nativo de la región de Los Tuxtlas, quien ha contribuido grandemente al conocimiento florístico de la Estación de Biología Tropical Los Tuxtlas Veracruz, del Instituto de Biología, UNAM.

**Inga skutchii** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 11. 1943. TIPO: Costa Rica: *Skutch 4823* (holotipo, F; isotipos, A, MO, US).

Especie muy poco colectada que se relaciona estrechamente con *Inga stenophylla* Standley, pero esta última cuenta con una flor más pequeña.

*Material representativo.* COSTA RICA. PUNTARENAS: *Liesner 1989* (MO). SAN JOSE: *Skutch 4823* (MO).

**Inga spectabilis** (M. Vahl) Willd., Sp. Pl. ed. 4, 4: 1017. 1806. Basiónimo: *Mimosa spectabilis* M. Vahl, Skr. Naturhist.-Selsk. 2: 219, t. 10. 1792. TIPO: Colombia: *von Rohr s.n.* (holotipo, C no localizado).

El tipo de Vahl fue colectado en Santa Marta, Colombia, por J. von Rohr; sin embargo, en las microfichas del Herbario de Vahl en Copenhague (C), no se ha localizado, por lo que de no encontrarse otro duplicado de von Rohr, se debe lectotipificar con la lámina de Vahl.

Especie muy característica de la cual León le creó su serie propia: *Spectabiles* León (1966). Se trata de una especie que muestra cierta variabilidad sobre todo del raquis foliar que va de terete a francamente alado.

Respecto a la variedad *schimpfii* Little basada en *Inga schimpfii* Harms (Repert. Sp. Nov. Regni Veg. 43: 112. 1938) del Ecuador y Perú, los isotipos en MO y US, así como otros ejemplares, parecen sostener a esta variedad geográfica, fundamentalmente discernible por caracteres de la inflorescencia y de las flores.

**Inga spectabilis** var. **spectabilis**

*Material representativo.* MEXICO. OAXACA: *Williams 9386* (F). TABASCO: *Chavelas P. et al. ES-2197* (MEXU). NICARAGUA. RIO SAN JUAN: *Moreno 23018* (MO). ZELAYA: *Moreno & Sandino 12754* (MO). COSTA RICA. ALAJUELA: *Liesner 14076* (MO). LIMON: *Stevens 24065* (MO). PUNTARENAS: *Davidse & Herrera Ch. 26301* (MO). SAN JOSE: *Dayton 3114* (MO). PANAMA. BOCAS DEL TORO: *Peterson & Annable 6665* (MO). COLON: *Holdridge & Maasola 6331* (MO). DARIEN: *Sytsma & D'Arcy 3471* (MO). CHIRIQUI: *Allen 1944* (MO). HERRERA: *Dwyer 2818* (MO). LOS SANTOS: *Dwyer 1210* (MO). SAN BLAS: *de Nevers 5976* (MO). ZONA DEL CANAL: *Croat 15044* (MO). COLOMBIA. ANTIOQUIA: *Archer 1428* (US). CHOCO: *Forero & Jaramillo 5304* (MO). HUILA: *Little 7924* (US). META: *Mejía et al. 1198* (US). VALLE: *Alston 8638* (BM). VENEZUELA. MERIDA: *Ruiz T. 601* (MO).

**Inga spectabilis** var. **schimpfii** (Harms) Little, Phytologia 19: 268. 1970.

*Material representativo.* ECUADOR. ESMERALDAS: *Little & Dixon 21191* (US). PERU. HUANUCO: *D. Smith 1301* (MO).

**Inga spiralis** Liesner et D'Arcy, Ann. Missouri Bot. Gard. 75: 385, fig. 2. 1988. TIPO: Panamá: *Mori & Kallunki 5577* (isotipo, MO).

Esta magna especie de *Inga* tiene su símil en *I. bullata* Benth. sensu stricto (sin incluir a *I. campanulata* Benth., como Bentham sugirió en 1876 y Taubert hizo en 1892), de la provincia de Rio de Janeiro en Brasil, pero la mantengo aparte, fundamentalmente porque ignoramos la morfología del fruto de *I. bullata*, además del enorme espacio

geográfico entre ambas entidades. También muestra afinidades con *I. jaunechensis* A. H. Gentry del Ecuador, pero difiere porque esta última cuenta con el pecíolo alado, las flores en espigas cortas, y el fruto curvo, pero no leñoso y circinado-espiralado.

*Material representativo.* PANAMA. PANAMA: *Dressler 4325* (MO). SAN BLAS: *Liesner 1314* (MO).

**Inga stenophylla** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 499. 1937. TIPO: Costa Rica: *Brenes 6841* (holotipo, F; isotipo, CR).

*Inga barbourii* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 55. 1944. TIPO: Costa Rica: *Barbour 1008* (holotipo, F; isotipos, MO, US).

Especie muy relacionada a *Inga skutchii* Standley (véase ésta), también tiene grandes semejanzas con *I. tenuipedunculata* León, con la que se le ha confundido. Con esta última, *I. stenophylla* difiere por su corola en general más larga, el cáliz más pequeño y más peloso, el mayor número en promedio de folíolos por hoja y el hecho que habita en un piso altitudinal superior.

El ejemplar de Nicaragua está estéril, por lo que su identificación es tentativa.

*Material representativo.* NICARAGUA. CHONTALES: *Gentry et al. 43944* (MO). COSTA RICA. ALAJUELA: *Brenes 11574* (NY). PANAMA. COCLE: *Knapp 1153* (MO).

**Inga tenella** M. Sousa, sp. nov. TIPO: México. Chiapas: km 18 Colonia Cuauhtemoc, Mpio. La Trinitaria, 15 abr. 1985, *Alush S. Ton 8185* (holotipo, MEXU; isotipo, MO).

Arbores medianae, ramis juvenilibus dense ferrugineo-tomentosis praeditae. Folis 3–4-jugata; stipulae 2.5–5 longae, ex ligulatae subulatae; foliola ex membranacea chartacea; rhachis foliaris alata, glandulis ex sessilibus longe stipitatis. Inflorescentiae spiciformes; pedunculus 1.8–4 cm longus; rachis floralis brevis; bracteae ex oblongae lineares. Flores sessiles; calyx 5–7 mm longus, tubularis-conicus, striatus; corolla 8–14 mm longa. Legumen usque ed 4 cm latum, ex complanatum subtetragonale, oblongum, ferrugineo-hirsutum.

Arboles (3–)5–20 m; ramas subanguladas a teretes, densamente ferrugíneo tomentosas cuando jóvenes, posteriormente glabrescentes. Hojas 6–8-folioladas; estípulas 2.5–5 mm, liguladas a subuladas, caducas; pecíolo 1–2(–4) cm, terete a marginado; folíolos concoloros, en ocasiones ligeramente discoloros, membranáceos a cartáceos, la base simétrica a ligeramente asimétrica, obtusa a cuneada, el ápice agudo a acuminado, en ocasiones cuspidado, el haz ligeramente brillante, moderadamente a esparcidamente piloso, el envés opaco, moderadamente piloso, la nervadura primaria eglandular; par basal de folíolos (2.3–)4.5–7 × (1.3–)2.1–3.3 cm, ovados a lanceolados, el par apical 7–14 × 3.1–6.5 cm, ovados a obovados, elípticos; raquis foliar 5.5–7.5(–9) cm, alado, el ala hasta 7 mm de ancho, elíptica a oblanceolada; glándulas interfoliolares sésiles a largamente estipitadas, clavuliformes, el cuerpo glandular 0.5–0.8 × 0.5–0.8 mm; apéndice ausente. Inflorescencias en espigas, 1–2 fasciculadas; pedúnculo 1.8–4 cm, ferrugíneo tomentoso; raquis floral 1–1.3 cm, las flores congestas, las brácteas homomorfas, 1.5–5 mm, concavas, oblongo-lineares a oblanceoladas, caducas. Flores sésiles; botones florales con el cáliz abierto; cáliz 5–7 mm, tubular-cónico, estriado, esparcidamente estrigoso a tomentoso, con escotaduras, los lóbulos 1.5–2 mm, triangulares; corola 8–14 mm, infundibuliforme, blanca, canescente vellosa; tubo estaminal inserto, blanco. Legumbre 7–14 × 3–4 × 0.8–1.5(–1.8) cm, aplanada a ocasionalmente subtetragonal, derecha a subespiralada, oblonga, sésil, apiculada en el ápice, ferrugíneo hirsuta, las valvas aplanadas, las suturas más o menos derechas, marginadas, los margenes de las suturas aplanados a 1-sulcados.

*Distribución y hábitat.* De Chiapas, México a Comayagua, Honduras, en áreas montañosas, en bosques caducifolios con *Liquidambar* (Hamamelidaceae), bosques de neblina y pinares. En altitudes entre 1,170 y 1,800 m, en ocasiones hasta 2,000 m. Florece en marzo y abril e inicia la fructificación en mayo y junio, los frutos persistiendo en al suelo hasta abril del siguiente año.

*Nombre vernáculo.* Sakil kok (Chiapas); cosós, cosoz (Honduras).

*Paratipos.* MEXICO. CHIAPAS: Mpio. La Trinitaria, 10 km ENE of Dos Lagos above Santa Elena, *D. E. Breedlove 56196* (MEXU). GUATEMALA. ALTA VERAPAZ: along Río Carchá, between Cobán and San Pedro Carchá, *P. C. Standley 89779* (A). BAJA VERAPAZ: 3 km SE of Purulhá, Sierra de las Minas, *L. O. Williams et al. 43415* (F). HONDURAS. COMAYAGUA: in ravine above El Achote, *D. Hazlett 1563* (MO); a 18 km al N de Otoro camino La Esperanza Siguatepec [Siguatepeque], *Martínez S. & Téllez V. 12816* (MEXU, TEFH); El Cedral, Cordillera Montecillos, *A. Molina R. 7206* (US); Cascada El Chorrito, 16 km al SO de Siguatepeque, *Molina R. 10907* (NY); Quebrada El Rincón, between El Portillo and El Porvenir, 10 km W of Siguatepeque, *Molina R. & Molina 25431* (BM); in a wet ravine near El Achote, hills above the plains of Siguatepeque, *T. G. Yuncker et al. 6292* (GH, MO). CORTES: Cofradía, montaña El Cusuco, *D. Ruiz 218* (TEFH). INTIBUCA: El Cedral, 20 km al SO de Siguatepeque, camino a Jesús de Otoro, *Molina R. 6153* (F, US); Calaveras, Cordillera de Opalaca, *Molina R. 6423* (F, GH, US); El Huise, entre km 10 y 13

carretera a Marcala, *Molina R. 13860* (NY, US); Los Baños de La Esperanza, *Molina R. 13928* (NY), *25533* (F, US); La Quebrada, El Huise, 9 km al E de La Esperanza, *Molina R. 14006* (NY, US); Cerro San Cristóbal, O de La Esperanza, *D. Ruiz 112* (NY, TEFH). LA PAZ: Quebrada El Cerrón, 8 km to Marcala, *Molina R. & A. R. Molina 24244* (NY), Catarata La Chorrera, 10 km N de Belén Gualcho, *C. Nelson et al. 3981* (MO).

*Inga tenella* M. Sousa pertenece al complejo de especies relacionadas con *I. villosissima* Benth. e *I. dasycarpa* M. Sousa (véase discusión de ésta); también se integra, en parte, con *I. cookii* Pittier (véase ésta). El epíteto se refiere a que dentro del grupo de especies a las que se relaciona, *I. tenella* es la que tiene la flor más chica, esbelta y frágil.

**Inga tenuipedunculata** León, Ann. Missouri Bot. Gard. 53: 308, fig. 3. 1966. TIPO: México. Veracruz: *Ll. Williams 9029* (holotipo, NY; isotipo, F).

Tanto en la clave como en la descripción de *Inga tenuipedunculata* León, la corola es citada como de 6–7 mm de largo; sin embargo, tanto en el tipo como en otras colecciones vistas por mí, la corola es más pequeña, de 4–6 mm de largo. Esto aunado a que en la clave León le da a la corola de *I. barbourii* Standley [= *I. stenophylla* Standley, véase ésta] como medida menos de 4 mm de largo, a pesar de que en el texto de la descripción él apunta como de 5–6 mm de largo, lo cual ha creado gran confusión en la determinación de estas especies.

*Inga tenuipedunculata* es una especie de las selvas altas perennifolias del sur de México a Costa Rica.

*Material representativo.* MEXICO. VERACRUZ: *Dorantes et al. 2956* (MEXU). NICARAGUA. MATAGALPA: *Neill 7258* (MO). COSTA RICA. ALAJUELA: *Herrera 1847* (MO).

**Inga thibaudiana** DC., Prodr. 2: 434. 1825. TIPO: Guayana Francesa: *Thibaud s.n.* (holotipo, G-DC).

*Inga peltadenia* Harms, Verh. Bot. Vereins Prov. Brandenburg 48: 160. 1907. TIPO: Perú: *Ule 6451* (holotipo, B, foto MO).

*Inga recordii* Britton et Rose in Standley, Trop. Woods 7: 5. 1929. TIPO: Belice: *Record s.n.* (holotipo, US, No. 1209905).

Una de las especies de *Inga* con mayor amplitud de distribución en selvas altas perennifolias. Aquí incluimos también a *I. peltadenia* Harms del Perú.

*Material representativo.* MEXICO. CHIAPAS: *Martínez S. 18333* (MEXU). BELICE. STANN CREEK: *Gentle 9197* (MEXU). TOLEDO: *Dwyer 13023* (MO). GUATEMALA. ALTA VERAPAZ: *Standley 90278* (F). IZABAL: *Marshall et al. 391* (MO). HONDURAS. CORTES: *Molina R. 10584* (F). GRACIAS A DIOS: *Nelson 849* (MO). OLANCHO: *Blackmore & Heath 1861* (BM). NICARAGUA. RIO SAN JUAN: *Moreno 23128A* (MO). ZELAYA: *Stevens 12745* (MO). COSTA RICA. HEREDIA: *Hammel & Robles 16693* (MO). LIMON: *Stevens et al. 24965* (MO). PUNTARENAS: *Utley & Utley 4869* (MO). SAN JOSE: *Skutch 4232* (A). PANAMA. BOCAS DEL TORO: *McPherson 12567* (MO). COCLE: *Dwyer 1874* (MO). COLON: *Dwyer 9542* (MO). DARIEN: *Dwyer 2226* (MO). PANAMA: *Dwyer 9444* (MO). SAN BLAS: *de Nevers & Herrera 3996* (MO). VERAGUAS: *McPherson 7190* (MO). ZONA DEL CANAL: *Nee 9693* (MO). TRINIDAD: *Schultes 18629* (US). COLOMBIA. AMAZONAS: *Gillett 16514* (US). ANTIOQUIA: *Shepherd s.n.* (MO). CHOCO: *Gentry & Fallen 17195* (MO). META: *Uribe-Uribe 861* (US). SANTANDER: *Gentry 15391* (MO). VALLE: *Cuatrecasas 14884* (US). VENEZUELA. BARINAS: *Valverde et al. 1214* (MO). BOLIVAR: *Aymard C. 4646* (MO). CARABOBO: *Pittier 8798* (US). MIRANDA: *González & Ortega 1366* (MO). SUCRE: *Steyermark & Liesner 120680* (MO). TACHIRA: *Gentry & Puig-Ross 14297* (MO). GUYANA: *de la Cruz 1595* (MO). SURINAME: *Stahel & Gongrijp 6241* (MO). GUAYANA FRANCESA: *Oldeman 1114* (MO). ECUADOR. ESMERALDAS: *Little 6302* (US). NAPO: *Palacios 2505* (MO). PERU. AMAZONAS: *Berlin 971* (MO). HUANUCO: *Schunke V. 1508* (US). MADRE DE DIOS: *Seibert 2166* (MO). LORETO: *Croat 19788* (MO). SAN MARTIN: *Schunke V. 8145* (MO). BOLIVIA: PANDO: *Sperling & King 6624* (US). BRASIL. (NORTE) ACRE: *Nelson 830* (US). AMAZONIA: *Pacheco et al. 92* (MO). PARA: *Sperling et al. 5920* (US). RONDONIA: *Nee 34909* (NY). RORAIMA: *Prance et al. 9998* (NY). (NORDESTE) BAHIA: *Salzmann s.n.* (MO). PERNAMBUCO: *Gentry et al. 50189* (MO). (SUDESTE) ESPIRITO SANTO: *Hatschbach 46783* (MO). MINAS GERAIS: *Heringer & Eiten 15188* (US).

**Inga tonduzii** J. D. Smith, Bot. Gaz. (Crawfordsville) 44: 112. 1907. TIPO: Costa Rica: *Tonduz 12928* (holotipo, US; isotipos, BM, K).

*Inga tonduzii* es cercana pero distinta de *I. barbata* Benth. de Brasil, la primera con brácteas, cáliz, y corola de mayor tamaño. Esta especie hasta hace poco era sólo conocida de Costa Rica, pero el ejemplar estéril de *Stevens 6886* de Nicaragua parece pertenecer a esta especie.

*Material representativo.* NICARAGUA. ZELAYA: *Stevens 6886* (MO). COSTA RICA. ALAJUELA: *Murphy 1363* (MO). CARTAGO: *Lent 1022* (MO). HEREDIA: *Chacón G. 986* (F). PUNTARENAS: *Utley & Utley 4913* (MO). SAN JOSE: *Burger & Stolze 5344* (NY).

**Inga umbellifera** (M. Vahl) Steudel, Nomencl. Bot. 1: 431. 1821. Basiónimo: *Mimosa umbellifera* M. Vahl, Ecolog. Amer. 3: 30. 1807. TIPO: América austral, *van Rohr s.n.* (holotipo, C, foto MO).

*Inga myriantha* Poeppig, Nov. Gen. Sp. Pl. 3: 77, t. 289. 1845. TIPO: Perú: *Poeppig 1097* (holotipo, W).

*Inga gracilipes* Standley, J. Wash. Acad. Sci. 15: 101.

1925. TIPO: Panamá: *Standley 30353* (holotipo, US).

*Inga lawranceana* Britton et Killip, Phytologia 1: 23. 1933. TIPO: Colombia: *Lawrance 260* (holotipo, US; isotipos, F, MO).

Aquí estoy considerando a *Inga umbellifera* en un sentido estricto sin incluir a *I. sciadion* Steudel, *I. umbratica* Poeppig, ni a *I. brevipes* Benth. (esta última no incluida en la sinonimia de León, 1966, ni por Poncy, 1985, para la Guayana Francesa), todas ellas con pedúnculos breves y otras combinaciones de caracteres que amplían el concepto de *I. umbellifera* a un punto de inmanejable; así que su delimitación requiere que se estudie con más cuidado el material sudamericano.

*Material representativo.* COSTA RICA. ALAJUELA: *Grayum 9052* (MO). HEREDIA: *Schubert & Holdridge 1302* (GH). LIMON: *Robles 2649* (MO). PUNTARENAS: *Gómez P. 22032* (MO). SAN JOSE: *Skutch & Barrantes 5059* (GH). PANAMA. COLON: *Croat 13178* (MO). DARIEN: *Knapp & Mallet 3056* (MO). PANAMA: *Miller et al. 853* (MO). SAN BLAS: *de Nevers & Marcus 3883* (MO). ZONA DEL CANAL: *Weaver & Foster 1597* (GH). COLOMBIA. AMAZONAS: *Schultes & Cabrera 16468* (US). ANTIOQUIA: *Shepherd 773* (MO). VENEZUELA. BOLIVAR: *Cardenas 870* (US). GUYANA: *Robinson 85-0106* (US). SURINAME: *Lanjouw & Lindeman 3019* (US). GUAYANA FRANCESA: *Mori & Pennington 17946* (MO). PERU. AMAZONAS: *Knapp & Alcorn 7701* (MO). JUNIN: *Stein & Todzia 2366* (MO). LORETO: *Rimachi Y. 3134* (MO). MADRE DE DIOS: *Gentry et al. 19629* (MO). SAN MARTIN: *Klug 3692*. UCAYALI: *Gentry & Díaz 58403* (MO). BRASIL. (NORTE) AMAZONIA: *Hill et al. 13043* (MO). PARA: *Silva & Bahía 3575* (MO).

**Inga urabensis** L. Uribe, Caldasia 4: 406. 1947. TIPO: Colombia: *O. Haught 4716* (isotipo, K).

*Inga cyclocarpa* Ducke, Arch. Jard. Bot. Rio de Janeiro 4: 14. 1925, non *I. cyclocarpa* (Jacq.) Willd., Sp. Pl. ed. 4, 4: 1026. 1806 [= *Enterolobium cyclocarpum* (Jacq.) Griseb.]. TIPO: Brasil: *Ducke RB10031* (sintipo, RB; isosintipo, B, foto MO).

*Inga callicarpa* Zamora, Brenesia 33: 99. 1991. TIPO: Costa Rica: *Hammel 13081* (holotipo, CR).

Esta especie fue primero descrita por Ducke (1925) pero debido a que desafortunadamente usó un homónimo tardío, el nombre de L. Uribe lo reemplaza. Aunque él no tuvo tal intención, y consecuentemente designó tipo.

Su afinidad es muy estrecha con *Inga venusta* Standley, de la cual, no es fácil de separar; ésto es más crítico en Colombia donde *I. venusta* adquiere folíolos de gran talla. En Mesoamérica las diferencias son un poco más claras, y aquí *I. venusta* se encuentra en un piso altitudinal mayor que *I. urabensis*.

*Material representativo.* COSTA RICA. HEREDIA: *Hammel 11658* (DUKE). LIMON: *Stevens 23736* (MO). PANAMA. BOCAS DEL TORO: *McPherson & Aranda 10159* (MO). SAN BLAS: *Sugden 619* (MO). COLOMBIA. ANTIOQUIA: *Hoyos & Hernández 705* (MO). BOYACA: *Lawrence 779* (K). CHOCO: *Forero & Jaramillo 4571* (MO). ECUADOR. PASTAZA: *Palacios & Neill 700* (MO). BRASIL. (NORTE) PARA: *Ducke RB10031* (B, foto, MO).

**Inga venusta** Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 500. 1937. TIPO: Costa Rica: *Brenes 6256* (holotipo, F; isotipo, CR).

*Inga venusta* está ubicada en el complejo de especies de flores amarillas, elevado a serie por León (1966): serie *Pilosulae* basada en *I. pilosula* (Rich.) J. F. Macbride; aquí agregamos la recientemente descrita *I. neblinensis* L. Cárdenas et G. De Martino. También muestra estrechas similitudes con *I. urabensis* L. Uribe (véase ésta).

*Material representativo.* COSTA RICA. ALAJUELA: *Herrera 1608* (MO). GUANACASTE: *Haber et al. 5577* (MO). PANAMA. COCLE: *McPherson 11263* (MO). COLON: *Mori & Kallunki 4895b* (LL). CHIRIQUI: *McPherson 9055* (MO). VERAGUAS: *McPherson 12814* (MO). COLOMBIA. CHOCO: *Gentry & Brand 36940* (MO). VALLE: *Gentry et al. 48361* (MO).

**Inga vera** Willd., Sp. Pl. ed. 4, 4: 1010. 1806. *Mimosa inga* L., Sp. Pl. 516. 1753, non. Vell. Conc. *Inga inga* (L.) Britton, Fl. Bermuda 170. 1918, nom. illeg. TIPO: Jamaica (lectotipo, Sloane, Voy. Jamaica 2: 58, t. 183, f. 1. 1725, designado aquí).

Para sinónimos véase León (1966) exceptuando a *Inga eriocarpa* Benth. e *I. xalapensis* Benth.

Con *Inga vera*, Willdenow creó un nombre dentro de *Inga* evitando el tautónomo que resultaría al usar el epíteto de Linneo, como lo hizo Britton posteriormente.

De *Mimosa inga* L. se ha reconocido desde Bentham (1845) que Linneo incluyó bajo este nombre a todas las especies relacionadas [serie *Inga*] que él conocía, incluyendo tres citas: Ray (Hist. Pl. 2: 1762. 1688), Sloane (Cat. Pl. Jamaica 153. 1696; Voy. Jamaica 2: 58, t. 183. fig. 1. 1725). Willdenow (1806) es el primero que la interpretó como lo que nosotros identificamos como *Inga edulis* C. Martius con material (P-H y B herb., B-W., IDC microficha no. 7440 microfoto 19020) y descripción que corresponden a dicha especie. Posteriormente Kunth (1824) adoptó esta determinación, la cual Bentham (1875) reconoció. El elemento de Linneo que podría caer bajo esta interpretación es la descripción de Ray (1688) por tratarse de una *Inga* del Brasil; sin embargo, en la descripción de la legumbre madura (la flor es desconocida) ésta es "compresa" y de 6.8–13.6

cm de largo, caracteres que no corresponden a *Inga edulis*. Por otro lado posteriormente Bentham (1875) estrechó los límites de *Mimosa inga* L. y de hecho pero no de forma la lectotipificó, apuntando que la "forma típica" es de Jamaica; así se reduce el problema a la segunda cita de Sloane. Linneo también citó al Hort. Cliff. 209, pero según F. Barrie (com. pers.) no existen ejemplares de herbario. Así, aquí se lectotipifica a *I. vera* con la lámina de Sloane, a pesar de que existen dos frutos en el herbario de Sloane, material del cual Linneo no tuvo acceso.

*Inga vera* es una especie muy polimorfa, que, muy problablemente agrupe a varias microespecies, que se han cruzado y ahora forman un complejo de híbridos, de los cuales no es posible delimitar taxa ni siquiera a nível infraespecífico. Sin embargo, los extremos de variación son reconocibles y en no pocos casos se presentan en las mismas áreas geográficas, haciendo difícil su separación en variedades geográficas o subespecies como León (1966) hizo. Así a guisa de ejemplo la muy característica variante de *Inga fissicalyx* Pittier, de cáliz grande con lóbulos largos y atenuados y corola cortamente exerta, es conocida principalmente del área de la vertiente del Golfo de México, de Veracruz al norte de Guatemala (área de *I. vera* subsp. *spuria*), pero aparece de nuevo (aunque con brácteas no tan largas) en el corazón de *Inga vera* subsp. *eriocarpa* (Benth.) León en Temascaltepec, Edo. de México (*Hinton 5572*, F) y en el área de *I. vera* Willd. subsp. *vera* en la República Dominicana (*Mejía & Zanoni 9062*, MO).

Es muy posible que el hombre haya ayudado grandemente a romper barreras entre las variantes originales, en vista que hoy en día se trata de un complejo con claras tendencias hacia "árboles maleza" de amplia distribución, particularmente en hábitats alterados.

La variación es muy notable en las flores así como las brácteas subyacentes, tanto en forma como en dimensiones y pelosidad; por otro lado las legumbres son bastante homogéneas.

Respecto a *Inga eriocarpa* Benth. (holotipo, *Coulter s.n.*, K) que León (1966) pasó a subespecie de *I. vera* Willd., el material más característico representativo (MEXICO. Colima: *Magallanes et al. 2815*, MEXU; Jalisco: *Mexía 1842*, BM, MO; Edo. México: *Hinton 5911*, F; Michoacán: *Emrick 22*, F; Morelos: *Muskus 20*, F; Nayarit: *Flores F. 1953*, MEXU) se parece más a *I. oerstediana* Benth. que a *I. vera*, tanto en hojas y glándulas interfoliolares como en pelosidad, pero con flores más robustas. Es muy posible que *I. eriocarpa* sea un híbrido entre *I. oerstediana* e *I. vera*. Ya Bentham (1875) consideró que *I. eriocarpa* podría ser la misma especie que *I. xalapensis* Benth. Sin embargo, *Inga eriocarpa* parece ser una buena especie que ha desarrollado una característica densa pelosidad lanuginosa en su cáliz y corola, diferente a la de sus postulados padres específicos, pero además *Inga eriocarpa* se está cruzando con *I. vera* produciendo todas las gradaciones tanto de glándulas interfoliolares como de tamaños de flores y formas de cáliz; un ejemplo de ello se muestra en los ejemplares del tipo de *I. oophylla* Riley (tipo, *González Ortega 250*, holotipo, K; isotipo, US).

Sobre la presencia de *I. eriocarpa* en Mesoamérica existen colecciones de Chiapas (*Goldman 858*, US; *Sousa et al. 11541*, MEXU) que tienen la pelosidad de *I. eriocarpa*, pero los demás caracteres se inclinan fuertemente hacia *I. vera*. Reconociendo que son posibles híbridos en donde dominan los caracteres de *I. vera*, por lo que no la estamos considerando para nuestra área.

Así *Inga vera* agrupa una gran variación no sólo por la cruza de sus variantes, sino también por cruzarse con *I. oerstediana* e *I. latibracteata* (véase *Inga* ×*xalapensis* Benth.), aumentando enormemente su variabilidad.

Con *Inga affinis* DC. (véase ésta) las similitudes también son grandes y sus diferencias son más bien de promedios que de calidad; sin embargo por el momento las mantengo separadas.

*Material representativo.* MEXICO. CAMPECHE: *Flores 10297* (XAL). CHIAPAS: *Martínez S. et al. 20162* (MEXU). COAHUILA: *Palmer 290* (GH). DURANGO: *H. Gentry 5317* (MO). GUERRERO: *Martínez S. & Morales 3507* (MEXU). HIDALGO: *Tenorio L. & Romero de T. 2517* (MEXU). JALISCO: *Bullock 1582* (MEXU). EDO. MEXICO: *Hinton 6205* (F). MICHOACAN: *Soto N. et al. 8589* (MEXU). NAYARIT: *Flores F. et al. 958* (MEXU). OAXACA: *Sousa et al. 6268* (MEXU). QUERETARO: *López Ch. 306* (IEB). QUINTANA ROO: *Sousa 12346* (MEXU). SAN LUIS POTOSI: *Seler 765* (GH). SINALOA: *Tenorio L. & Romero de T. 13698* (MEXU). TABASCO: *Sousa et al. 11740* (MEXU). TAMAULIPAS: *Valiente et al. 145* (MEXU). VERACRUZ: *Purpus 1917* (F). BELICE. AUGUSTINE: *Hunt 465* (MO). BELIZE: *Liesner & Dwyer 1650* (MO). EL CAYO: *Balick et al. 1921* (MO). GUATEMALA. ALTA VERAPAZ: *Tenorio et al. 14480* (MEXU). BAJA VERAPAZ: *Harmon & Dwyer 3023* (MO). CHIQUIMULA: *Téllez V. & Martínez S. 8879* (MEXU). EL PETEN: *Tún Ortíz 1750* (F). ESCUINTLA: *Tonduz & Rojas 48* (MO). GUATEMALA: *J. D. Smith 2316* (US). HUEHUETENANGO: *Steyermark 51550* (F). IZABAL: *Jones et al. 3198* (F). JALAPA: *Standley 76751* (F). QUEZALTENANGO: *J. D. Smith 2822* (US). RETALHULEU: *Standley 88784* (MO). SACATEPEQUEZ: *Rojas 348* (US). SANTA ROSA: *Standley 79177* (F). SOLOLA: *Kellermann 5883* (US). SUCHITIPEQUEZ: *Steyermark 47803* (F). ZACAPA: *Steyermark 42136* (F). HONDURAS. ATLANTIDA: *Yuncker et al. 8333* (MO). COLON: *Saunders 879* (MO). COMAYAGUA: *Dueñas 57* (MO). CORTES: *Nelson et al. 2879* (MO). CHOLUTECA: *Espinal O. 196* (MO). GRACIAS

A DIOS: *Gentry et al. 7504* (MO). EL PARAISO: *Martínez S. & Téllez V. 12813* (MEXU). MORAZÁN: *Píneda 167* (MO). OCOTEPEQUE: *Nelson et al. 1494* (MO). OLANCHO: *Chévez 170* (MO). SANTA BARBARA: *Padilla 34* (MO). EL SALVADOR. AHUACHAPAN: *Croat 42167* (MO). CABANAS: *Calderón 1587* (US). LA LIBERTAD: *Standley 23236* (GH). LA UNION: *Standley 20935* (US). SAN MIGUEL: *Standley 21142* (GH). SAN SALVADOR: *Calderón 1565* (NY). SAN VICENTE: *Standley 21674* (GH). SANTA ANA: *Carlson 765* (F). SONSONATE: *Pittier 1928* (US). NICARAGUA. CARAZO: *Grijalva & Almanza 3572* (MO). CHINANDEGA: *Robleto 1818* (MO). CHONTALES: *Stevens & Montiel 19137* (MO). GRANADA: *Grijalva & Araquistain 717* (MO). ESTELI: *Moreno 8141* (MO). JINOTEGA: *Moreno 16419* (MO). LEON: *Grijalva 2381* (MO). MADRIZ: *MacQueen & Styles 1* (MEXU). MANAGUA: *Sandino 2561* (MO). MASAYA: *Calderón et al. 70* (MO). MATAGALPA: *Neill 1997* (MO). NUEVA SEGOVIA: *Neill 1660* (MO). RIO SAN JUAN: *Sandino 3607* (MO). RIVAS: *Moreno 22092* (MO). ZELAYA: *Neill 4087* (MO). COSTA RICA. ALAJUELA: *Brenes 20471* (F). CARTAGO: *Stork 2111* (F). GUANACASTE: *Sousa et al. 12754* (MEXU). HEREDIA: *Pittier & Tonduz 2515* (US). PUNTARENAS: *Khan et al. 1157* (BM). SAN JOSE: *Skutch 4695* (NY). PANAMA. COCLE: *Folson & Kauke 2773* (MO). DARIEN: *Lazor & Correa 3402* (MO). HERRERA: *Allen 4069* (MO). LOS SANTOS: *Stern et al. 33678* (MO). PANAMA: *Dressler 3352* (MO). VERAGUAS: *Folsom et al. 2478* (MO). ZONA DEL CANAL: *Nee & Tyson 10894* (MO). CUBA: *Shafer 12420* (MO). JAMAICA: *Proctor 37341* (MO). PUERTO RICO: *Duke 7346* (MO). HAITI: *Nash 337* (F). REPUBLICA DOMINICANA: *Mejía & Zanoni 9062* (MO). COLOMBIA. CHOCO: *Duke 11014* (MO). GUAJIRA: *Arboleda et al. 420* (MO). SANTA MARTA: *H. H. Smith 106* (MO). VALLE: *Alston 7950* (F). VENEZUELA. ARAGUA: *Pittier 12299* (F). DELTA AMACURO: *Rusby & Squires 194* (MO). GUARICO: *Aristeguieta 7032* (MO). PORTUGUESA: *Aymard 94* (MO). MERIDA: *Liesner & González 10611* (MO). ZULIA: *Davidse et al. 18638* (MO).

**Inga ×xalapensis** Benth. (pro sp.), London J. Bot. 4: 616. 1845. TIPO: México. Veracruz: *Linden 671* (holotipo, K).

*Inga ×zacuapanica* Harms (pro sp.), Repert. Spec. Nov. Regni Veg. 19: 63. 1923. TIPO: México. Veracruz: *Purpus 3684* (isotipos, F, MO, US).

Aquí se está postulando que *Inga xalapensis* Benth. y su sinónimo *I. zacuapanica* Harms son de origen híbrido entre *I. vera* Willd. e *I. latibracteata* Harms; se trata de una hibridización muy común que aún no se estabiliza, y por tanto hay ejemplares intermedios y otros más cercanos a uno u otro progenitor; sin embargo, los más comunes son con hojas similares a *I. vera*, pero con la bráctea floral grande y ancha de *I. latibracteata* y la flor de tamaño intermedio a chica y de las proporciones de *I. latibracteata*. La glándula interfoliolar varia de una a otra, predominando la de cavidad grande de *I. latibracteata*.

Estos híbridos se presentan a casi todo lo largo de la distribución de *Inga latibracteata*, extendiendose *I. ×xalapensis* más al sur hasta el oeste de Honduras.

*Material representativo.* MEXICO. CHIAPAS: *Ton 1794* (F). HIDALGO: *Hernández M. & Rodríguez B. 5695* (MEXU). OAXACA: *Conzatti 3487* (MEXU). PUEBLA: *Patrón & Basurto 60* (MEXU). VERACRUZ: *Purpus 8765* (MO). GUATEMALA. ALTA VERAPAZ: *Molina R. & Molina 12113* (F). HONDURAS. OCOTEPEQUE: *Molina R. 24184* (BM).

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# REVISION DEL GENERO *STYPHNOLOBIUM* (LEGUMINOSAE: PAPILIONOIDEAE: SOPHOREAE)[1]

*Mario Sousa S.*[2] *y Velva E. Rudd*[3]

## Resumen

Se confirma la segregación de *Styphnolobium* de *Sophora* en base a su hábitat, estipelas, bractéolas, legumbre y número cromosómico. Se amplian sus límites de cuatro a nueve especies, al describirse cinco nuevas especies para la ciencia: *Styphnolobium burseroides*, *S. monteviridis*, *S. parviflorum*, *S. protantherum*, y *S. sporadicum*. Se reconocen dos secciones, haciendose una nueva combinación: sección *Oresbios*. El género se centra en el área mexicano-mesoamericana. Se muestra su cercana afinidad con *Calia* en base a el hábito, bractéolas, y dehiscencia de la legumbre.

## Abstract

The genus *Styphnolobium* is recognized as a segregate from *Sophora* on the basis of habit, stipels, bracteoles, legume, and chromosome number. It is enlarged from four to nine species through the description of five species new to science: *Styphnolobium burseroides*, *S. monteviridis*, *S. parviflorum*, *S. protantherum*, and *S. sporadicum*. Two sections are recognized, one requiring the new combination section *Oresbios*. The genus is centered in the Mexican-Mesoamerican area. Through similarities in habit, bracteoles, and dehiscence of the legume, it is clearly most closely related to *Calia*.

El género *Styphnolobium* (Leguminosae: Papilionoideae: Sophoreae) fue creado por Schott (1830) a partir de *Sophora japonica* L., pero ha sido considerado frecuentemente como parte de *Sophora*, como en la última revisión del género por Tsoong & Ma (1981). Sin embargo Bentham (1837, 1839) y Burkart (1952) lo reconocen, aunque el primero posteriormente (1865) modificó radicalmente su criterio, o bien, existe el consenso de asignarle una categoría propia, así Yakovlev (1964) lo colocó como sección, que reconoce Rudd (1972) y como subgénero Tsoong en Tsoong & Ma (1981). Después Yakovlev (1967) cambió de opinión y lo reconoció como género aparte, reviviendo también a *Calia* Berlandier.

El concepto de este grupo como unidad, bajo las diferentes categorías que ya apuntamos, en realidad ha incluido solamente a dos especies *Sophora japonica* L. (*Styphnolobium japonicum*) del sureste de Asia y *S. affinis* Torrey et A. Gray (*Styphnolobium affine*) del sureste de los Estados Unidos, pero en los últimos años han empezado a aparecer nuevas especies para la ciencia en México y Centro América que corresponden a este grupo

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(véase Sousa, 1990). Se totalizan hasta el momento nueve especies, que en conjunto permiten ahora evaluar mejor el problema al aumentar en varias veces la variabilidad conocida. Así decidimos estudiar el grupo desde diferentes puntos de vista, invitando a G. Palomino y a sus alumnas Patricia Martínez y Carmen Bernal (Bernal & Martínez, 1989), para ver el problema de los cariotipos y números cromosómicos, que a la vez ella logró que E. Martínez O. viera el polen, sus resultados son dados en el artículo que sigue a éste (Palomino et al., 1993).

Ya sea que la posición, sea dentro de *Sophora* o fuera, *Styphnolobium* mantiene varios caracteres propios distintivos y reconocibles, también es claro que está cercanamente relacionado a *Sophora* sensu lato particularmente a *Calia* como proponen en diferentes grados Yakovlev (1967, 1968), Tsoong & Ma (1981), y Polhill (1981).

Así podemos resumir sus diferencias con la siguiente clave:

1a. Herbaceas perennes, arbustos o árboles; flores ebracteoladas; legumbre dehiscente. ..... *Sophora*
1b. Arboles; flores bracteoladas; legumbre indehiscente.
2a. Hojas sin estipelas; cáliz bilabiado, el labio vexilar más largo que el carinal; legumbre con pericarpio seco; $2n = 18$. ..... *Calia*
2b. Hojas estipeladas; cáliz trunco o casi trunco, si bilabiado, el labio vexilar más corto que el carinal; legumbre con epicarpio coriáceo, mesocarpio y endocarpio carnosos; $2n = 28$. ..... *Styphnolobium*

Concordando en principio con Yakovlev (1967, 1968), separandolas en tres grupos, estando muy cercanamente relacionado a *Calia*, aunque no bajo la misma categoría como proponen Tsoong & Ma (1981), los que las incluyen bajo el subgénero *Styphnolobium*, incluyendo además a *Sophora pachycapa* Schrenk ex C. A. Meyer del Asia Menor, la cual es totalmente diferente en hábito además de que carece de estipelas y bractéolas, caracteres propios de *Sophora* sensu stricto.

Además de los caracteres morfológicos, los números cromosómicos de seis de las nueve especies conocidas de *Styphnolobium* presentan un número de $2n = 28$ (Palomino et al., 1993, artículo que sigue); contrastando con $2n = 18$ tanto para *Sophora* como para *Calia*. Resulta muy sugestivo el hecho que en las Sophoreae de Norte América existan dos géneros más con número diploíde de $2n = 28$, es decir *Cladrastis* y *Pickeringia* (véase Goldblatt, 1981) éste último considerado de posición incierta y frecuentemente colocado, aunque con reticencia, en las Thermopsidae por su similitud en las hojas (Turner, 1981).

Por otro lado, si comparamos morfológicamente a *Styphnolobium*, *Cladrastis*, y *Pickeringia* no resultan tan diferentes en cuanto a su tipo básico de inflorescencia (Fig. 1A–G). También muestran claras cercanias con *Calia*, asi tanto *Pickeringia* y varias especies de *Calia* presentan gradaciones de flores francamente solitarias en las axilas de las hojas a racimos, esto ya había sido observado por Nuttall (1840) en *Pickeringia*. La gradación va de hojas 3-folioladas cuyos folíolos laterales se reducen grandemente y constituyen las bractéolas y el folíolo terminal o central que funge como la bráctea floral subyacente al pedicelo. En cuanto a *Cladrastis* debido a lo efímero de sus diminutas bractéolas, no son descritas y en general se interpretan como carentes; su legumbre dehiscente, aplanada y delgada lo diferencia.

Dentro de las Sophoreae pero ya no en el grupo *Sophora* (Polhill, 1981), sino en el grupo *Dussia*, *Dussia*, en el único conteo reportado por Goldblatt (1981), presenta tambien $2n = 28$. Aquí se trata de un género con francas relaciones fitogeográficas hacia Sudamérica, que sin embargo comparte más caracteres con el grupo *Styphnolobium* que con *Sophora* sensu stricto.

Al aumentar dramáticamente el conocimiento de la variabilidad de *Styphnolobium* es posible sugerir tendencias evolutivas en el género (véase Tabla 1); así de su análisis *Styphnolobium affine* resultó la única especie que cuenta con todas las fases primitivas de los nueve caracteres tratados. Por otro lado ninguna posee todas las fases avanzadas de los caracteres usados: la que conjuntó más fue *S. burseroides* y en base a estos caracteres es que arreglamos las especies en el tratamiento sistemático, aunque con limitaciones, ya que en algunas especies faltó el conocimiento de estructuras o estadios como son las plántulas.

Sobre su fitogeografía Sousa y Delgado (en prensa) dan una relación que aquí modificamos en vista de la nueva información obtenida. Sus especies tienden a ser endémicos restringidos (Fig. 2), que actualmente habitan en climas templados a cálidos y de subdesérticos a húmedos.

Existen, afortunadamente, varios registros fósiles de frutos y folíolos asociados de la Formación Claiborne (Herendeen & Dilcher, 1986; Herendeen, 1990, 1992), fechados del Eoceno Medio del occidente de Kentucky y Tennessee y asociados a bosques que contaban con: Podocarpaceae, Theaceae, Anacardiaceae, Magnoliaceae, Hamamelidaceae, Moraceae, Sapotaceae, Annonaceae, Nys-

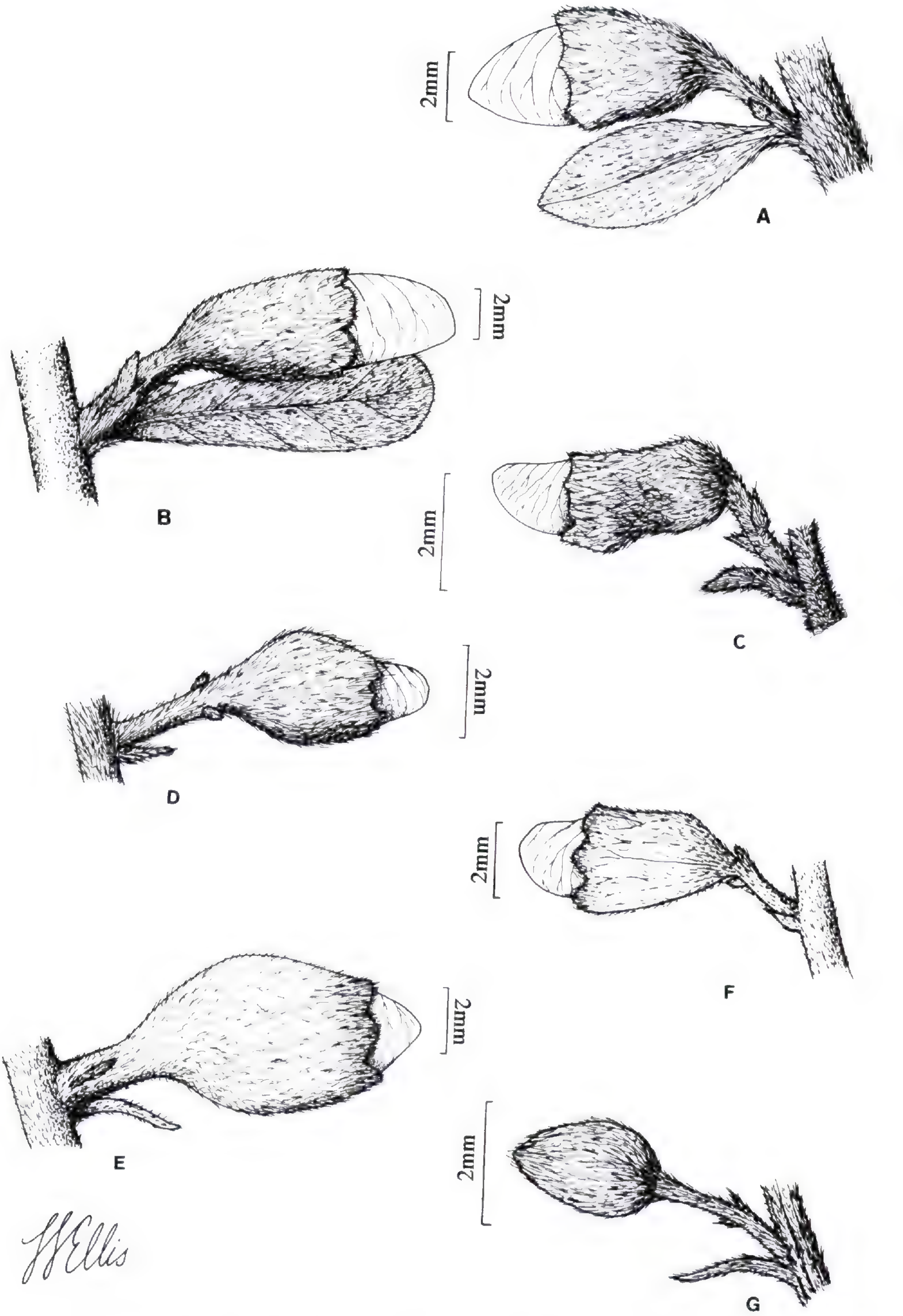


FIGURA 1. Botones florales mostrando bráctea floral y bractéolas.—A. *Pickeringia montana*. (Tomado de *McMurphy 80*, MO.)—B. *Sophora* (*Calia*) *gypsophyla* var. *guadalupensis*. (Tomado de *Burgess 1764*, MO.)—C. *Styphnolobium burseroides*. (Tomado de *Guízar N. 1343*, MEXU.)—D. *Styphnolobium affine*. (Tomado de *Palmer 6264*, MO.)—E. *Styphnolobium conzattii*. (Tomado de *R. Torres C. 5231*, MEXU.)—F. *Styphnolobium japonicum*. (Tomado de *Slama 43*, MO.)—G. *Cladrastis kentukea*. (Tomado de *Palmer 24856*, MO.)

TABLA 1. Tendencias evolutivas en *Styphnolobium*.

| Primitivos | Avanzados |
|---|---|
| Estipelas bien desarrolladas | Estipelas muy reducidas a faltantes |
| Inflorescencia axilar, racemosa | Inflorescencia terminal, paniculada |
| Cáliz no giboso | Cáliz giboso |
| Cáliz 5-dentado | Cáliz trunco o casi trunco |
| Polen con la exina de retículo abierto | Polen con la exina de retículo cerrado |
| Ovario peloso | Ovario glabro |
| Legumbre homogenea | Legumbre con marcas |
| Germinación con los cotiledones epigeos | Germinación con los cotiledones hipogeos |
| Eófilos bien desarrollados | Eófilos reducidos a catáfilos |

saceae, Lauraceae, Fagaceae, Juglandaceae, Myricaceae, Rhamnaceae, Euphorbiaceae, y otras. Esta composición florística de la vegetación se acerca mucho a los bosques caducifolios o mesófilos de montaña que actualmente habitan las vertientes húmedas de las sierras del sur de México al norte de Nicaragua. Sin embargo, dada la abundancia, diversidad, y grupos de leguminosas conocidas (Herendeen, 1990, 1992) y considerando lo pobre en leguminosas que actualmente este tipo de vegetación posee, es posible que también habían otros tipos de vegetación menos húmedos y más cálidos, como selvas medianas a altas subperennifolias y aún más estacionales, francamente caducifolias con abundantes mimosoideas como los depositos atestiguan, y no necesariamente confinado a áreas templadas como Herendeen (1992) sugiere.

Por lo anterior, la naturaleza de endemismo en este género es de paleoendémicos, en los que el representante asiatico muestra ya caracteres avanzados y únicos en el género, como el polen y el tipo de inflorescencia; sus parientes americanos parecen ser sus predecesores, siendo *Styphnolobium affine* el posible puente entre la rama asiatica y la rama americana del género.

**Styphnolobium** Schott, Wiener Z. Kunst. 3: 844. 1830. Sinónimo: *Sophora* secc. *Styphnolobium* (Schott) Yakovlev, Trudy Leningradsk. Khim.-Farm. Inst. 17: 56. 1964. Homónimo tardío: Tsoong, Acta Phytotax. Sin. 19(2): 161. 1981. ESPECIE TIPO: *Styphnolobium japonicum* (L.) Schott.

Arboles; corteza lisa, fisurada a escamosa placoide irregular, en ocasiones exfoliante, con tonos metálicos; el crecimiento en brotes cortos y largos, frecuentemente ramifica en los cortos y las ramas tienden a parecer casi verticiladas. Hojas alternas, estipuladas, 1-pinnadas, imparipinnadas, los folíolos generalmente opuestos proximalmente y marcadamente alternos distalmente o todos opuestos o alternos, estipelados. Inflorescencias racemosas, axilares, raramente terminales y paniculadas; flores pediceladas, los pedicelos articulados basalmente, con una bráctea subyacente subamplexicaule en la base; bractéolas presentes, 2; hipantio desarrollado; cáliz lobado a truncado, giboso o no giboso; corola papilionoidea, polipétala, rosado pálido a blanquecina, glabra, pétalos unguiculados; lámina del estandarte suborbicular, reflexa, maculada; alas simétricas a asimétricas, sin rugosidades; pétalos de la quilla libres y ampliamente traslapados; estambres libres; anteras uniformes; ovario glabro a peloso, estilo glabro; estigma terminal, atenuado. Legumbre indehiscente, suculenta, moniliforme a torulosa, péndula, frecuentemente estipitada por aborción de las semillas proximales, homogénea o con marcas lisas en el margen vexilar, exocarpo coriáceo, mesocarpo y endocarpo carnoso y mucilaginoso; semillas oblongo-elipsoideas, lisas, negruzcas a negras, con el hilo lateral, con el endospermo cubriendo al embrión y la radícula incurvada. Plántulas con los cotiledones epigeos o raramente hipogeos, las primeras hojas por encima de los cotiledones (eófilos) alternas en ocasiones subopuestas, imparipinnadas o raramente reducidas a catáfilos. $2n = 28$.

CLAVE PARA LAS SECCIONES DE *STYPHNOLOBIUM*

1a. Inflorescencia terminal, paniculada. ..... Sección 1. *Styphnolobium*

1b. Inflorescencia axilar, racemosa, en ocasiones tenuemente se ramifica. ..... Sección 2. *Oresbios*

SECCION 1.

## Styphnolobium.

Arboles; inflorescencia terminal, paniculada; polen con la exina de retículo cerrado. Una especie del sureste de Asia.

**Styphnolobium japonicum** (L.) Schott, Wiener Z. Kunst. 3: 844. 1830. Basiónimo: *Sophora japonica* L., Mant. Pl. 1: 68. 1767. TIPO: Japón (aparentemente introducida), *Kleynhoff s.n.* Para sinónimos véase Rudd, 1972. Figura 1F.

Arboles hasta 25 m; ramas glabras, esparcidamente lenticeladas. Hojas 7–17-folioladas; estípulas 3–4 mm, linear-atenuadas, pronto caducas; pecíolo 1.4–3.5 cm; raquis foliar 5.5–25 cm; fo-

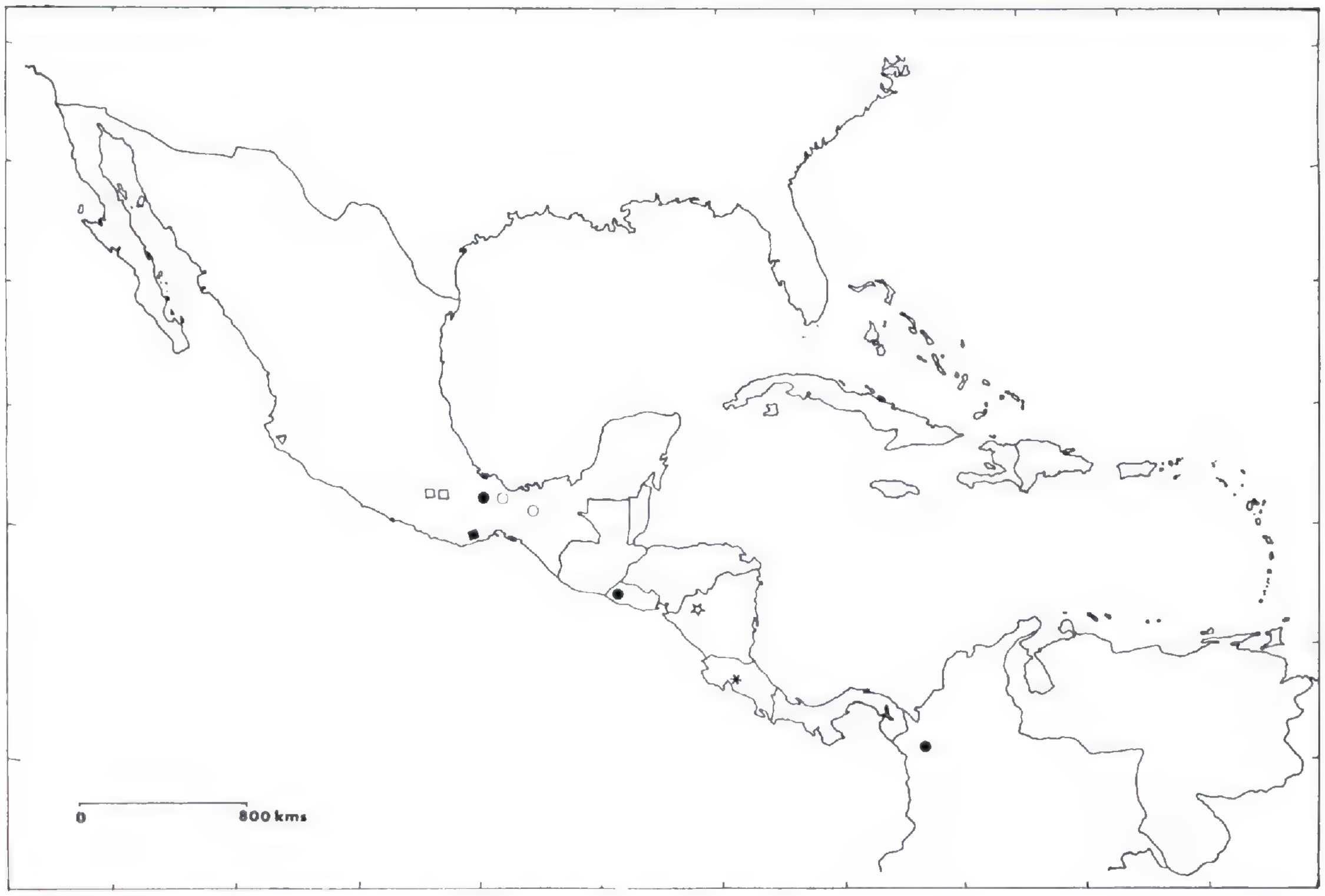


FIGURA 2. Mapa de distribución de las especies mexicano-mesoamericanas de *Styphnolobium*. —Triángulo invertido, *S. protantherum*. —Cuadrados, *S. burseroides*. —Círculos, *S. parviflorum*. —Círculos llenos, *S. sporadium*. —Cuadrado lleno, *S. conzattii*. —Estrella, *S. caudatum*. —Asterisco, *S. monteviridis*.

líolos alternos a subopuestos, estipelados, las estipelas ca. 1 mm, aciculares, subpersistentes; láminas 1–6 × 0.5–2.5 cm, lanceoladas, la base obtusa en ocasiones aguda, el ápice acuminado a agudo, el haz glabrescente, el envés esparcidamente canescente seríceo, en ocasiones glauco. Inflorescencias terminales, en panículas; floración tardía; ejes secundarios 3.5–17 cm; bráctea 1–1.5 mm, triangular-atenuada, caduca; pedicelo 3 mm, articulado apicalmente, esparcidamente diminutamente canescente seríceo; bractéolas ca. 1 mm, triangular-atenuadas, cercanas al cáliz, pronto caducas; flores 12–15 mm; cáliz 3–4 mm, ciatiforme, no giboso, glabrescente excepto moderada a densamente canescente seríceo sobre los lóbulos y margen, 5-lobado, los lóbulos hasta 1.2 mm, redondeados; pétalos blancos a amarillo pálido; estandarte largamente unguiculado, la uña hasta 4 mm; ovario esparcidamente amarillento seríceo. Legumbre 3–12 × 0.7–1 cm, moniliforme, homogénea, glabrescente, excepto esparcidamente canescente serícea en el estípete, constricciones y rostro, estipitada, el estípite hasta 1.7 cm; semillas 0.8 × 0.4–0.5 cm, 1–8 por fruto. Plántulas con los cotiledones epigeos, los eófilos imparipinnados, en ocasiones 1-foliolados o 3-foliolados. $2n = 28$.

*Distribución y hábitat.* Esta especie aparentemente es sólo nativa de China, pero desde hace mucho se ha cultivado y naturalizado en Japón, de donde originalmente se describió, en la actualidad se le cultiva ampliamente en el mundo. Se trata de un árbol caducifolio que florece en agosto–septiembre y fructifica en octubre–noviembre en China.

*Material representativo.* CHINA. ANHUI: *K. Yao 8472* (MO). CHENGJIANG: *Yao & Kan 79360* (MO). HUBRI: *E. H. Wilson 2558* (MO). JIANGRI: *K. Yao 9113* (MO). XIZANG: *G. Forrest 24754* (MO). YUNNAN: *A. Henry 9871* (US).

El ejemplar anotado como *Sophora japonica* en el Herbario de Linneo LINN 522.9 no es *S. japonica*, y si es *Sophora* se parece más a *S. tomentosa* L.

Para fines de esta revisión no se estan considerando los taxa infraespecíficos descritos para esta especie, para ello véase el trabajo de *Sophora* de Tsoong & Ma (1981).

*Styphnolobium japonicum* muestra el carácter único en el género de inflorescencia terminal en panícula y sus relaciones más cercanas parecen ser con *S. affine*.

SECCION 2.

***Oresbios*** (Rudd) M. Sousa et Rudd, comb. nov. Basiónimo: *Sophora* secc. *Oresbios* Rudd, Phytologia 21(5): 327. 1971. ESPECIE TIPO: *Styphnolobium conzattii* (Standley) M. Sousa et Rudd.

Arboles; inflorescencia axilar, racemosa; polen con la exina de retículo abierto. Ocho especies de América del Norte y Mesoamérica, extendiéndose una a Colombia.

CLAVE PARA LAS ESPECIES DE *STYPHNOLOBIUM* SECC. *ORESBIOS*

1a. Legumbre moniliforme, 0.7–1 cm de diámetro, con 1–8 semillas. (Texas, Oklahoma, Arkansas, y Louisiana, Estados Unidos.) ..... 1. *S. affine*
1b. Legumbre torulosa a moniliforme 1.6 2.8 cm de diámetro, con 1–3(–4) semillas. (Centro de México al Norte de Sudamérica.)
2a. Legumbre ferrugíneo velutina o canescente-serícea al menos en el estípite; ovario canescente o pardo-amarillento seríceo.
3a. Legumbre homogénea sin marcas en el margen vexilar.
4a. Folíolos coriáceos; estipelas bien desarrolladas; folíolos redondeados a corto acuminados en el ápice; inflorescencias 2.5 6 cm, flores con cáliz 5–6 mm. (Oaxaca, México.) ..... 2. *S. conzattii*
4b. Folíolos cartáceos; estipelas poco desarrolladas; folíolos largamente acuminados a caudados en el ápice; inflorescencias 6.5 17 cm, flores con cáliz 3.5–4 mm. (Nicaragua.) ..... 3. *S. caudatum*
3b. Legumbre con marcas ocres (lisas al secarse) en el margen vexilar.
5a. Hojas 15–21-folioladas, folíolos 1.5–3 × 0.8–1.5 cm, canescente tomentoso en el envés; cáliz someramente 5-lobado. (S del Desierto de Tehuacán, Oaxaca, y Puebla, México.) 8. *S. burseroides*
5b. Hojas 7 11-folioladas, folíolos 5 6.5 × 2–3.3 cm, glabrescentes en el envés; cáliz casi trunco. (Costa de Jalisco, México.) ..... 6. *S. protantherum*
2b. Legumbre glabra; ovario glabro.
6a. Cáliz 5-lobado; hojas 13–17-folioladas. (Monteverde, Costa Rica.) ..... 4. *S. monteviridis*
6b. Cáliz trunco; hojas 5–13-folioladas.
7a. Flores 11–13 mm; hojas 5–7-folioladas. (Sur de Veracruz, México.) ..... 5. *S. parviflorum*
7b. Flores 15–20 mm; hojas 9–13-folioladas. (S. México a Colombia.) ..... 7. *S. sporadicum*

**1. Styphnolobium affine** (Torrey et A. Gray) Walp., Repert. Bot. Syst. 1: 807. 1843. Basiónimo: *Sophora affinis* Torrey et A. Gray, Fl. N. Amer. 1(3): 390. 1840. TIPO: Estados Unidos. Louisiana, Red River, *Leavenworth s.n.* (lectotipo, designado por Rudd (1972), NY). Figura 1D.

Arbustos a árboles 2–5(–10) m; ramas esparcidamente canescente seríceas a tomentulosas cuando jóvenes, pronto glabras, esparcidamente lenticeladas. Hojas (9–)13–19-folioladas; estípulas ca. 2 mm, lineares, pronto caducas; pecíolo 1.2–3.5 cm; raquis foliar 4.5–13.5 cm; folíolos alternos, frecuentemente opuestos, estipelados, las estipelas 1 mm, lineares, pronto caducas; láminas 1–4.5 × 0.5–2.5 cm, elípticas en ocasiones ovadas u obovadas, la base aguda en ocasiones algo cuneada a obtusa, el ápice obtuso a agudo, el haz glabro a glabrescente, el envés esparcidamente canescente seríceo. Inflorescencias axilares; floración tardía; pedúnculo 0.5–2 cm; raquis floral 2–8 cm; bractéolas 0.2–0.5 mm, lineares, frecuentemente distantes del cáliz, pronto caducas; flores 13–16 mm; cáliz 3–4 mm, ciatiforme, no giboso, esparcidamente canescente seríceo, 5-lobado, los lóbulos hasta 1 mm; pétalos blancos a lila, en ocasiones matizados de púrpura, glabros; estandarte largamente unguiculado, la uña hasta 3.5 mm; ovario densamente canescente seríceo. Legumbre 3–6 (–15) × 0.7–1 cm, moniliforme, homogénea, glabra excepto canescente serícea en el estípite, constricciones y rostro, estipitada, el estípite hasta 1.5 cm; semillas 0.6–0.7 × 0.4–0.5 cm, 1–4 por fruto. Plántulas con los cotiledones epigeos, los eófilos imparipinnados. $2n = 28$.

*Distribución y hábitat.* Conocida del sureste de los Estados Unidos en los estados de Texas, Oklahoma, Arkansas, y Louisiana, en bosques caducifolios con *Ulmus*, *Bumelia*, *Celtis*, *Crataegus*, *Diospyros*, y *Fraxinus*; en bosques de *Quercus* y en praderas; frecuentemente en suelos derivados de calizas o alcalinos. Florece de finales de marzo a mayo y fructifica de agosto a noviembre.

*Nombres vernáculos.* Eve's necklace, necklace tree.

*Material representativo.* ESTADOS UNIDOS. ARKANSAS: *B. F. Bush 2487* (MO), *G. W. Letterman s.n.* (MO), *E. J. Palmer 9396*, (MO), *26719* (MO). LOUISIANA: *J. W. Thieret 21142* (LL). OKLAHOMA: *W. H. Emig 797* (MO), *G. J. Goodman 5460* (TEX), *S. Hagen s.n.* (MO), *M. Hopkins & M. Rogers 3976* (MO, TEX), *E. L. Little 36246* (MO), *E. J. Palmer 10473* (MO), *24047* (MO). TEXAS: *D. S. Correll 15919* (LL), *V. L. Cory 43021* (TEX), *54769* (LL), *D. Chesser s.n.* (TEX), *C. L. Lundell*

*& Lundell 10285* (LL), *D. Lynch s.n.* (TEX), *A. Ruth 355* (US), *626* (US), *L. D. Smith 385* (US), *H. H. York 128d* (TEX), *46257* (TEX).

**2. Styphnolobium conzattii** (Standley) M. Sousa et Rudd, Ann. Missouri Bot. Gard. 77(3): 575. 1990. Basiónimo: *Sophora conzattii* Standley, Contr. U.S. Natl. Herb. 23(2): 436. 1922. *Calia conzattii* (Standley) Yakovlev, Trudy Leningradsk. Khim.-Farm. Inst. 21(4): 45. 1967. TIPO: México. Oaxaca: *Conzatti et al. 3171* (holotipo, US; isotipo, MEXU herbario Conzatti). Figuras 1E, 2, y 3.

Arboles 22–25 m; corteza placoide; ramas canescente velutinas a tomentulosas cuando jóvenes, pronto glabrescentes, esparcidamente lenticeladas. Hojas 5–9-folioladas; estípulas ca. 0.8 mm, linear-aleznadas, pronto caducas; pecíolo 2–5 cm; raquis foliar 4–10.5 cm; folíolos opuestos a casi opuestos en ocasiones los distales alternos, estipelados, las estipelas 1–2 mm, recurvadas, crasas, persistentes; láminas 3.5–5.5(–7.5) × 2.2–3.5(–4.5) cm, coriáceas, ovadas, elíptico-ovadas a anchamente elípticas, la base obtusa a aguda, el ápice obtuso a agudo, el haz y envés glabros. Inflorescencias axilares; floración tardía; pedúnculo muy reducido hasta 0.8 cm, raquis floral 2.5–5.5 cm; bráctea ca. 1 mm, triangular-atenuada, pronto caduca; bractéolas ca. 0.6 mm, oblongas, pronto caducas; flores 20–25 mm; cáliz 5–6 mm, infundibuliforme, ligeramente giboso, ferrugíneo seríceo; casi trunco; pétalos violeta, glabros; estandarte largamente unguiculado, la uña hasta 4 mm; ovario canescente seríceo. Legumbre 6.5–14 × 2.2–2.5 cm, torulosa, homogénea, canescente sericea, densamente en el estípite, constricciones y rostro, esparcidamente a la altura de las semillas, estipitada, el estípite hasta 2.5 cm; semillas 2 × 1.4 cm, 1–3 semillas por fruto. $2n = 28$.

*Distribución y hábitat.* Especie endémica del Cerro Espino en la Sierra Madre del Sur, Oaxaca, México, en altitudes entre 1,150 y 1,200 m, poco común en selvas medianas perennifolias, en suelos rocosos. Florece de abril a mayo y cuenta con frutos maduros en abril del año siguiente.

*Nombres vernáculos.* Frijolillo, granadillo.

*Material representativo.* MEXICO. OAXACA: *Sousa 5598* (MEXU), *Torres C. 4901* (MEXU, MO), *5231* (MEXU, MO).

Esta especie es muy característica por sus hojas coriáceas; estipelas persistentes, crasas y recurvadas; y las flores grandes.

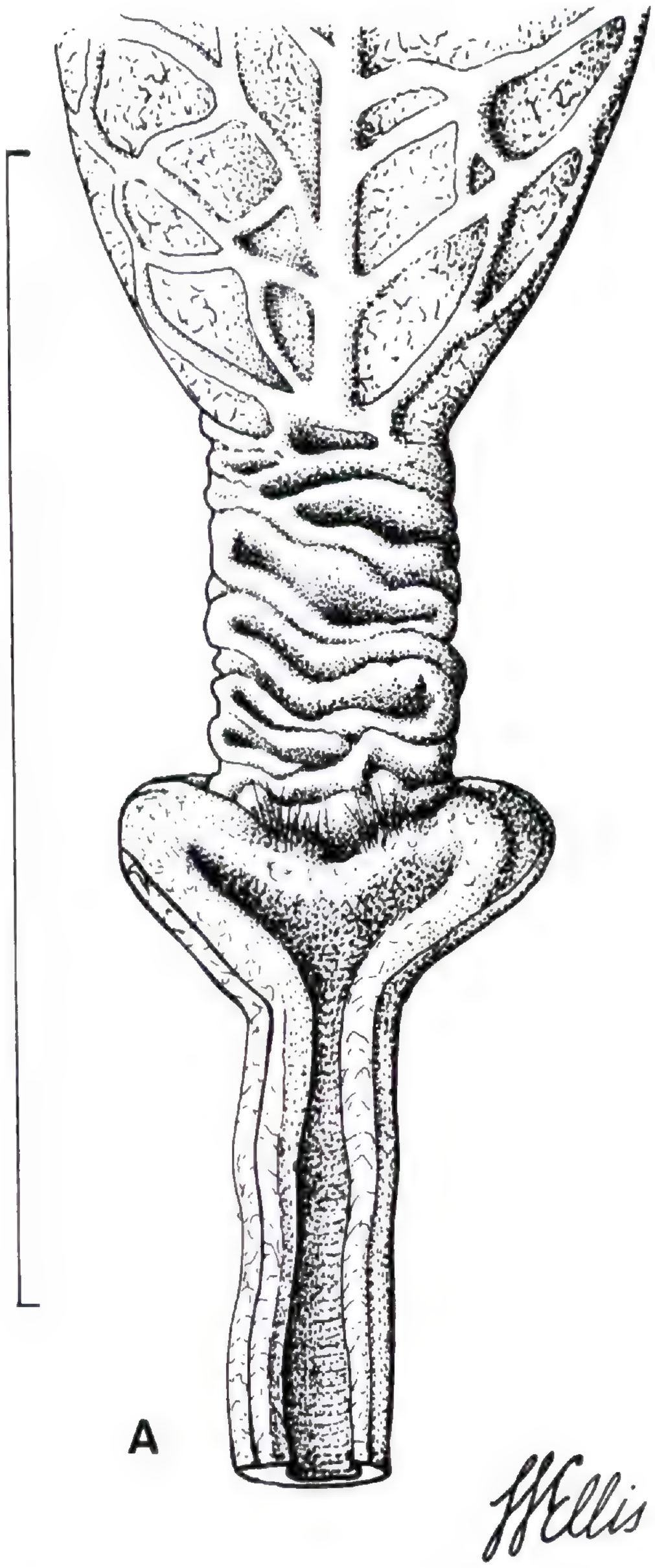


FIGURA 3. *Styphnolobium conzattii.*—A. Base de folíolo terminal, mostrando estipelas prominentes y pulvínulo. (Tomado de *R. Torres C. 5231.*)

**3. Styphnolobium caudatum** M. Sousa et Rudd, Ann. Missouri Bot. Gard. 77: 573, fig. 1. 1990. TIPO: Nicaragua: *Sousa et al. 12985* (holotipo, MEXU; isotipos, BM, HNMN, MO). Figura 2.

Arboles de más de 30 m; corteza escamosa placoide irregular, con tonos metálicos, con abundantes lenticelas prominentes; ramas diminutamente canescente seríceas cuando jóvenes, pronto esparcidamente, esparcida a moderadamente lenticela-

das. Hojas 9–13-folioladas; estípulas desconocidas; pecíolo 2.5–5.5 cm; raquis foliar 7–15 cm; folíolos alternos, estipelados, las estipelas hasta 0.8 mm, oblongas, pronto caducas; láminas 4–9 × (1.3–)2–2.7 cm, lanceoladas, la base redondeada ligeramente asimétrica, en ocasiones cuneada, el ápice largamente acuminado a caudado, el haz glabro, el envés esparcidamente seríceo. Inflorescencias axilares, en ocasiones algo paniculadas, 12–17 cm; pedicelo 5–9 mm; cáliz (en frutos inmaduros) 3.5–4 mm, giboso, pardo velutino, casi trunco. Legumbre 5–14 × 2.3–2.7 cm, torulosa, homogénea, densamente ferrugíneo velutina, estipitada, el estípite hasta 4 cm; 1–2(–4) semillas por fruto (semillas maduras no fueron vistas).

*Distribución y hábitat.* Sólo se conoce de la localidad tipo en Estelí, Nicaragua, de un sólo árbol, en una cañada húmeda, en la vega de un río, a 900 m de altitud. Con frutos inmaduros durante mayo.

*Material representativo.* NICARAGUA. ESTELI: *P. P. Moreno 25655* (MEXU, MO).

**4. Styphnolobium monteviridis** M. Sousa et Rudd, sp. nov. TIPO: Costa Rica. Puntarenas: Monteverde, Pacific slope, 10°18′N, 84°48′O, 1,450 m, *W. Haber 9118* (holotipo, MEXU; isotipo, MO). Figura 2.

Arbores magni, folia proterantha, 13–17 foliolata, foliolis lanceolatis vel ellipticis, glabris. Inflorescentiae axillares, pedunculi ad 1.2 cm longi, rhachides florales (3.5–)5–11 cm longae; bracteoli diminuti, decurrentes, caducei; flores mediani; calyx infundibuliformis, gibbosus, 5-lobatus; vexillum unguiculatum; ovarium glabrum. Legumina homogenea, glabra, 1–2(–4) seminibus onusta.

Arboles (15–)30–40 m; ramas esparcidamente canescente pilosas cuando jovenes, pronto glabras, moderado a densamente lenticelado-verrugosas. Hojas 13–17-folioladas; estípulas ca. 3 mm, linear-atenuadas, pronto caducas; pecíolo 2.5–6 cm; raquis foliar 9–15 cm; folíolos alternos a subopuestos proximalmente, estipelados, las estipelas ca. 1 mm, linear-liguladas, pronto caducas; láminas 3.2–6 × 2.2–2.5 cm, lanceoladas a elípticas, la base obtusa a aguda, el ápice acuminado, el haz y envés glabros. Inflorescencias axilares; floración tardía; pedúnculo muy reducido hasta 1.2 cm; raquis floral (3.5–)11 cm; bráctea 3–4 mm, linear-aleznada, pronto caduca; pedícelo 4–6 mm, pardo velutino; bractéolas ca. 0.2 mm, lineares, decurrentes por 1 mm, pronto caducas; flores ca. 20 mm; cáliz 7 mm, anchamente infundibuliforme, giboso, pardo seríceo a velutino, 5-lobado, los lóbulos ca. 1 mm, apiculados; pétalos lavanda con nervaciones oscuras; estandarte largamente unguiculado, la uña hasta 6 mm; ovario glabro. Legumbre (inmadura) 5.5–9(–13) × 2.2 cm, torulosa, homogénea, glabra, estipitada, el estípite hasta 2.5 cm, glabro; semillas (inmaduras) 2 × 1.7 cm, 1–2(–4) por fruto. Plántulas se desconocen.

*Distribución y hábitat.* Esta especie sólo se conoce del área de Monteverde, Costa Rica, en altitudes entre 1,400 y 1,550 m. Florece a mediados de febrero y a finales de julio, el período de fructificación aún se desconoce, pero a finales de agosto ya cuenta con frutos bastante desarrollados pero aún inmaduros.

*Paratipos.* COSTA RICA. PUNTARENAS: Monteverde, 10°47′N, 84°50′O, *A. Gentry & W. Haber 48728* (MO); 10°18′N, 84°43′O, *B. Hammel 17037* (MO); along road to Eston Rockwell farm, *G. S. Hartshorn 1898* (MO, NY).

Esta especie pertenece al grupo de *Styphnolobium* con ovario glabro, legumbre homogénea. El epíteto se refiere a Monteverde, área que es muy rica en endemismos.

**5. Styphnolobium parviflorum** M. Sousa et Rudd, sp. nov. TIPO: México. Veracruz: Estación de Biología Tropical Los Tuxtlas, U.N.A.M., Mpio. San Andrés Tuxtla, 150 m altitud, en selva alta perennifolia, suelo arcilloso, 9 enero 1974, *M. Sousa 4299* (holotipo, MEXU; isotipo, MO). Figuras 2 y 4.

Arbores magni; folia proterantha 5–7 foliolata, foliolis ovatis, oblongis vel late ellipties, glabris. Inflorescentiae axillares; pedunculi ad 1 cm longi, rhachides florales 1–4 cm longae; bracteoli parvi, ligulati, caducei; flores parvi; calyx infundibuliformis, agibbosum, truncatus; vexillum longe unguiculatum; ovarium glabrum. Legumina homogenea, glabra, 1(–2) seminibus onusta. Cotyledones epigaeae.

Arboles 22–35 m; ramas canescente seríceas cuando jóvenes, pronto glabras, moderadamente lenticelado-verrugosas. Hojas 5–7-folioladas; estípulas ca. 1.5 mm, lineares, pronto caducas; pecíolo 2.5–4 cm, raquis foliar 2.5–6.5 cm, folíolos opuestos a alternos, estipelados, las estipelas ca. 1.2 mm, lineares, pronto caducas; láminas 3.5–8.5 × (1.7–)2.2–4 cm, ovadas, oblongas a anchamente elípticas, la base obtusa, el ápice obtuso a apiculado en ocasiones acuminado, el haz y envés glabros. Inflorescencias axilares; floración tardía; pedúnculo muy reducido hasta 1 cm; raquis floral 1–4 cm; bráctea ca. 2.5 mm, angostamente triangular-atenuada, pronto caduca; pedicelo 2–4.5 mm, pardo seríceo, bractéolas ca. 0.5 mm, liguladas, pronto caducas; flores 11–13 mm; cáliz 3–4 mm, infundibuliforme, no giboso, pardo seríceo, trunco a casi trunco; pétalos blancos a rosado pálido; estandarte

FIGURA 4. *Styphnolobium parviflorum* M. Sousa et Rudd. A. Rama con inflorescencias.—B. Cáliz pedicelado con bráctea y bractéolas.—C. Estandarte. -D. Ala.—E. Pétalo de la quilla.—F. Gineceo y androceo. (Tomados de *Ponce y Cedillo T. 6.*)—G. Legumbre. (Tomado de *Calzada 994.*)—H. Semilla. (Tomada de *Sousa 4299.*)—I. Plántula. (Tomada de *Calzada 994.*)

largamente unguiculado, la uña hasta 4 mm; ovario glabro. Legumbre 4.5–11 × 3.5–4 cm, torulosa, homogénea, glabra, sésil a estipitada, el estípite hasta 3 cm; semillas 2.8 × 1.8–2 cm, 1(–2) por fruto. Plántulas con los cotilédones epigeos, los eófilos imparipinnados; 5–9(–10)-foliolados; $2n = 28$.

*Distribución y hábitat.* Conocida solamente de dos áreas del estado de Veracruz, la región de Los Tuxtlas y la zona de Uxpanapa, en vegetación

de selvas altas perennifolias a subperennifolias, formando parte del dosel de la selva con *Brosimum alicastrum* Sw., *Simira salvadorensis* (Standley) Steyerm. y *Pseudobombax* sp. en litosoles calizos y en suelos negros pedregosos de origen volcánico. En altitudes entre 100 y 250 m. Florece de principios de diciembre a la primera quincena de enero, la fructificación se inicia en febrero, habiendo frutos maduros hasta mayo.

*Nombres vernáculos.* Melaza, melcocha, palo de melcocha.

*Paratipos.* MEXICO. VERACRUZ: Mpio. Jesús Carranza: 0.5 km al N del Poblado 2, 17°15′30″N, 94°40′O, *T. Wendt et al. 5282* (MEXU); Mpio. San Andrés Tuxtla, Estación de Biología Tropical Los Tuxtlas, U.N.A.M., 18°34′–18°36′N, 95°09′O, *J. I. Calzada 994* (MEXU, MO), *1112* (MEXU), *1752* (MEXU), *G. Ibarra M. 615* (MEXU), *778* (MEXU), *1099* (MEXU), *1299* (MEXU, MO), *F. Ponce & R. Cedillo Trigos 6* (MEXU), *S. Sinaca C. & F. Chigo S. 729* (MEXU, MO); Laguna Escondida, a 3 km al NO de la Estación de Biología Tropical Los Tuxtlas, *Sinaca C. 708* (MEXU, MO).

Especie que cuenta con varios caracteres avanzados en el género, tales como cáliz trunco o casi trunco, ovario y legumbre glabras, reducción del número de folíolos, los cuales en plántula son más numerosos que en las hojas de los ejemplares arbóreos y flores pequeñas, por este último carácter se nombra a esta especie.

**6. Styphnolobium protantherum** M. Sousa et Rudd, sp. nov. TIPO: México. Jalisco: entrada a Cuenca 3, Estación de Investigación, Experimentación y Difusión Chamela, U.N.A.M., Mpio. La Huerta, 24 febrero 1984, *J. Arturo S. Magallanes 4159* (holotipo, MEXU). Figuras 2 y 5.

Arbores mediani vel magni; folia 9–11 foliolata, foliolis ovatis, late ellipticis, glabrescentibus vel glabris. Inflorescentiae axillares, interdum paniculatae; flores praecoces, mediani; pedunculi 1.4–3.5 cm longi; rhachides florales 7–13 cm longae; bracteoli parvi, lineari-attenuati; calyx infundibuliformis, paullo gibbosus, subtruncatus, ovarium sericeum. Legumina maculis ochraceis, laevibus praedita, 1–2(–4) seminibus onusta. Cotyledones epigaeae.

Arboles 12–25 m; corteza longitudinalmente fisurada que forma placas; ramas canescente seríceas cuando jóvenes, pronto glabras, esparcidamente lenticeladas. Hojas 9–11-folioladas; estípulas ca. 1.6 mm, linear-aleznadas, pronto caducas; pecíolo 1.8–4 cm; raquis foliar 8–11(–13) cm; folíolos opuestos a alternos, estipelados, las estipelas 0.4–0.6 mm, triangular-atenudas, pronto caducas; láminas 3–6.5 × 1.8–3.2 cm, ovadas, anchamente elípticas, en ocasiones elípticas u obovadas, la base obtusa, el ápice obtuso, apiculado a cortamente acuminado, el haz y envés esparcidamente canescente seríceos, pronto glabros. Inflorescencias axilares en ocasiones paniculadas; floración precoz; pedúnculo 1.4–3.5 cm, raquis floral 7–13 cm; bráctea ca. 1.5 mm, angostamente triangular-atenuada, pronto caduca; pedicelo 3–3.5 mm, pardo seríceo; bractéolas ca. 1 mm, linear-atenuadas, pronto caducas; flores 14–16 mm; cáliz 4–6 mm, infundibuliforme, algo giboso, pardo seríceo, casi trunco; pétalos rosados; estandarte largamente unguiculado, la uña hasta 5 mm; alas algo asimétricas; ovario densamente canescente seríceo. Legumbre 4–12.5(–15.5) × 2–2.5 cm, torulosa, con marcas ocres y lisas en el margen vexilar, glabra excepto serícea en el estípite, estipitada, el estípite hasta 2.6 cm; semillas 2.5 × 1.5 cm, 1–2(–4) por fruto. Plántulas con los cotiledones epigeos, los eófilos imparipinnados, 7–9-foliolados. $2n = 28$.

*Distribución y hábitat.* Sólo conocida de la costa de Jalisco en selvas medianas subperennifolias a subcaducifolias, en suelos metamórficos. En altitudes alrededor de los 800 m. En el período de sequía esta especie es caducifolia y florece sin hojas a finales de febrero a principios de marzo, fructifica a partir de marzo contando con frutos maduros en mayo.

*Paratipos.* MEXICO. JALISCO: Mpio. La Huerta, Estación de Biología, Chamela, U.N.A.M., E of Eje Central, *Bullock 1495* (MEXU, MO); Arroyo el Zarco, *J. A. S. Magallanes 990* (MEXU, MO); Estación de Biología, Chamela, *Magallanes 2177* (MEXU, MO); entrada a la Cuenca 3, *4179* (MEXU); Vereda Buho, *4237* (MEXU, MO).

*Styphnolobium protantherum* muestra ciertas afinidades con *S. burseroides*, pero es marcadamente diferente (véase clave); su epíteto hace énfasis en su floración previa a la producción de hojas en la estación seca.

**7. Styphnolobium sporadicum** M. Sousa et Rudd, sp. nov. TIPO: Colombia. Antioquia: Mpio. de Venecia: 4.2 km E of Bolombolo on road to Venecia, Hacienda La Plata, 06°01′N, 75°48′W, 920 m, *J. L. Zarucchi & B. Echeverry 4666* (holotipo, MO; isotipos, CR, HUA no vistos, K, MEXU, US). Figura 2.

Arbores mediani; vel magni. Folia proterantha, 9–13 foliolata, foliolis ovatis, ellipticis vel ovato-ellipticis. Inflorescenciae axillares, pedunculi ad 1 cm longi, rhachides florales 1.5–8(–11) cm longae; bracteoli parvi; flores mediani; calyx infundibuliformis, paullo gibbosus, fere truncatus; ovarium glabrum. Legumina homogenea, glabra, 1–2 seminibus onusta.

Arboles 18–30 m; ramas esparcidamente canescente seríceas cuando jóvenes, pronto glabras,

FIGURA 5. *Styphnolobium protantherum* M. Sousa et Rudd.—A. Ramas con hojas y flores. (Con hojas tomado de *Magallanes 2177*, con flores de *Bullock 1495*.)—B. Flor sin pétalos mostrando pedicelo, bractéolas, cáliz, gineceo, y androceo.—C. Estandarte.—D. Ala.—E. Pétalo de la quilla.—F. Legumbre mostrando las marcas vexilares.—G. Plántula. (Flor, frutos, y plántula tomados de *Bullock 1495*.)

esparcida a densamente lenticelado-verrugosas. Hojas 9–13-folioladas; estípulas ca. 1 mm, triangular-atenuadas a liguladas, pronto caducas; pecíolo 3.5–5.5 cm; raquis foliar 9 13 cm; folíolos alternos, estipelados, las estipelas 0.6–0.8 mm, liguladas, pronto caducas; láminas (4–)6–9.5(–11.5) × 3.5–4(–5) cm, ovadas, elípticas a ovado-lanceoladas, la base obtusa a aguda en ocasiones

cuneada, el ápice acuminado a cortamente acuminado, el haz y envés glabros. Inflorescencias axilares; floración tardía; pedúnculo muy reducido hasta 1 cm; raquis floral 1.5–8(–11) cm; bráctea 1–1.5 mm, triangular-aleznada a linear-aleznada; bractéolas muy reducidas, pronto caducas; flores 15–16 mm; cáliz 4–6 mm, infundibuliforme, algo giboso, pardo a cinéreo velutino, casi trunco; pétalos rosado pálido a purpúreos; estandarte largamente unguiculado, la uña hasta 4 mm; ovario glabro. Legumbre 4.2–10 × 2.2–2.7 cm, torulosa, homogénea, glabra, sésil a estipitada, el estípite hasta 2.5 cm; semillas (maduras se desconocen), 1–2 por fruto. Plántulas se desconocen.

*Distribución y hábitat.* Esta especie aparentemente tiene una distribución amplia y esporádica, en selvas altas subperennifolias con *Brosimum alicastrum* Sw. sobre litosoles calizos en altitudes entre 50 y 500 m, en el norte de Oaxaca, México; en altitudes entre 300 y 600 m en la reserva de El Imposible en El Salvador; en selvas medianas caducifolias a 920 m, en el Valle del Río Cauca, Antioquia, Colombia. Florece en marzo y fructifica en el norte de Oaxaca a finales de mayo y en El Salvador a finales de noviembre.

*Nombres vernáculos.* Almendrillo, almendrillo de montaña (en El Salvador).

*Paratipos.* MEXICO. OAXACA: Distr. Tuxtepec, Mpio. Santa María Jacatepec, camino a Cosolapa San Antonio, Ejido de San Felipe Tilpa, 13.3 km al SO de La Reforma, *R. Torres 12168* (MEXU); Mpio. Santa María Soyaltepec, lado sur del vertedor de la Presa Temazcal, *L. Cortés et al. 237* (MEXU, MO). EL SALVADOR. AHUACHAPAN: Hacienda El Imposible, *D. A. Cáceres 39* (MEXU), *J. A. Tablas s.n.* (MEXU).

Esta especie es la que tiene la distribución más amplia del género, y por lo incompleto del material (se desconocen sus flores) en su límite norte en Oaxaca, Mexico, es díficil precisar si en realidad estamos tratando solamente con una sola entidad taxonómica o dos; sin embargo, por los caracteres disponibles no nos es posible separarlas convincentemente. El epíteto hace referencia a la distribución esporádica de esta especie.

**8. Styphnolobium burseroides** M. Sousa, Rudd et Medrano, sp. nov. TIPO: México. Puebla: 7 km al sur de Molcaxac, 1,800 m altitud, en selva baja caducifolia sobre ladera caliza, 9 junio 1984, *F. González Medrano 14126* (holotipo, MEXU; isotipos, MEXU, MO). Figuras 1C, 2, y 6.

Arbores parvi; folia 15–21 foliolata, foliolis ovalis, oblongis, vel late ellipticis, subtus arachnoidei-canescentibus. Inflorescentiae axillares; flores coaetanei, mediani; calyx valde gibbosus, 5-lobatus; ovarium sericeum. Legumina maculis ochraceis, laevibus praedita, subra semina glabescentia. Plantulae hypogaeae, eophyllis cataphyllis reductis.

Arboles 4–10 m; corteza externa escamosa, exfoliante; ramas densamente canescente velutinas a tomentosas cuando jóvenes, pronto glabrescentes. Hojas 15–21-folioladas; estípulas 2–3 mm, angostamente triangular-atenuadas, pronto caducas; pecíolo 0.2–1 cm; raquis 6–10.5 cm; folíolos alternos a opuestos, en ocasiones estipelados, las estipelas 0.4–0.6 mm, liguladas, frecuentemente faltan; láminas 1.4–2.2 × 0.7–1.2 cm, ovadas, oblongas a anchamente elípticas, la base obtusa, el ápice obtuso, apiculado a mucronulato, el haz canescente velutino a piloso, el envés canescente aracnoideo. Inflorescencias axilares; floración coetánea; pedúnculo muy reducido a nulo; raquis floral 1.2–4 cm; bráctea ca. 2 mm, linear-oblanceolada; pedicelo 2–3 mm, densamente canescente velutino a piloso; bractéolas 0.5–0.6 mm, lineares, pronto caducas; flores 14–15 mm; cáliz 5–6 mm, ciatiforme, marcadamente giboso, esparcidamente canescente piloso, más densamente sobre los lóbulos, 5-lobado, los lóbulos hasta 1 mm, triangulares; pétalos rosados, excepto el estandarte que es blanco con máculas verde-amarillentas; estandarte largamente unguiculado, la uña hasta 4.5 mm; ovario densamente canescente seríceo. Legumbre 4–10.5 × 1.6–1.7 cm, torulosa, con marcas ocres y lisas en el margen vexilar, esparcidamente pilosa a glabrescente excepto sericea en el estípite, constricciones y rostro, estipitada, el estípite hasta 2 cm; semillas 2.3–2.5 × 1.4 cm, 1–2(–3) por fruto. Plántulas con los cotiledones hipogeos, los eófilos reducidos a catáfilos. $2n = 28$.

*Distribución y hábitat.* Endémico de la región sur del Desierto de Tehuacán, en los estados de Oaxaca y Puebla en México, en vegetación de selvas bajas caducifolias con *Cephalocereus* sp., *Bursera* spp., *Acacia coulteri*, *Actinocheita filicina* (Sessé et Mociño) Barkley, *Leucaena*, y *Wimmeria*, en matorrales esclerófilos con *Actinocheita*, *Rhus*, y *Brahea* siempre sobre suelos someros, negros, de origen calizo, en altitudes entre 1,520 y 1,900 m. Florece en marzo y junio y fructifica en julio y marzo.

*Paratipo.* MEXICO. OAXACA: Distr. Huajuapan de León, Yucumduchi, 10 km al N de Huajuapan en los límites de Puebla–Oaxaca, *A. García M. & R. Torres C. 1442* (MEXU); Distr. Teposcolula, a 3 km al NO de Tamazulapán, carr. Tamazulapán–Huajuapan de León, *E. Matuda 28424* (MEXU, MO). PUEBLA: Mpio. Huehuetlán, *P. Tenorio L. & A. Salinas 11539* (MEXU,

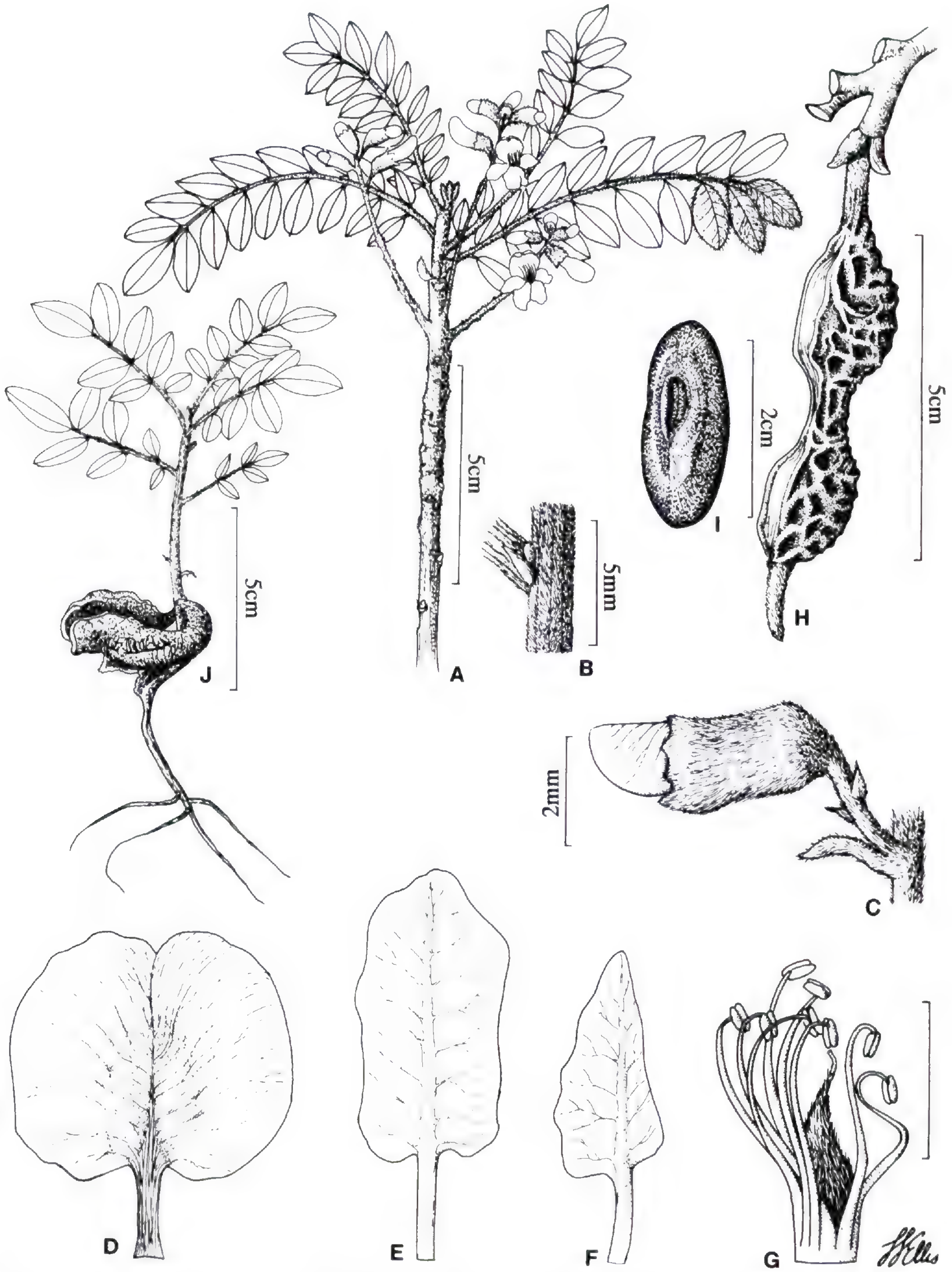


FIGURA 6. *Styphnolobium burseroides* M. Sousa, Rudd et Medrano.—A. Rama con inflorescencias.—B. Detalle de estípula.—C. Botón floral mostrando bráctea floral, bractéolas, y cáliz giboso, lobulado. (Tomadas de *González Medrano 14126.*)—D. Estandarte. —E. Ala. —F. Pétalo de la quilla. G. Gineceo y androceo. (Tomados de *Guízar N. 1343.*)—H. Legumbre mostrando las marcas vexilares. (Tomado de *Sousa 11952.*)—I. Semilla. (Tomada de *Guizar N. 1343.*)—J. Plántula. (Tomada de *Sousa 11959.*)

MO); Mpio. Izúcar de Matamoros, paraje Infiernillo, 12 km al SE de Raboso, dentro de la cuenca Vistahermosa, *E. Guizar N. 1343* (MEXU); Mpio. Molcaxac, 8–19 km al S de Molcaxac, carr. hacia San Juan Ixcaquixtla, *F. Chiang & A. Valiente 2005* (MEXU, MO), *Chiang et al. 2149* (MEXU), *F. González Medrano et al. 11727* (MEXU), *M. Sousa et al. 11952* (MEXU), *11959* (MEXU).

Especie muy característica tanto por la pelosidad en sus hojas, su cáliz fuertemente giboso y dentado, las contrastantes marcas de sus frutos, y las plántulas con cotiledones hipogeos y los eófilos reducidos. El nombre específico aduce a su superficial semejanza con el género *Bursera* tanto en sus hojas, como en su corteza que se exfolia.

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# DIFERENCIAS CROMOSOMICAS ENTRE ALGUNAS ESPECIES DE LOS GENEROS *SOPHORA* L. Y *STYPHNOLOBIUM* SCHOTT[1]

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## Resumen

En este estudio se determinó el número cromosómico ($2n$) y cariotipo de *Sophora secundiflora*, *S. velutina* var. *zimbabweensis*, *S. tomentosa*, *Styphnolobium japonicum*, *S. parviflorum*, *S. protantherum*, *S. burseroides*, y *S. conzattii*. Las tres primeras presentaron un $2n = 18$, un número básico $x = 9$, pequeñas variaciones en sus cariotipos, y un par de cromosomas con constricción secundaria. Las cinco especies restantes, mostraron $2n = 28$, $x = 14$; sus cariotipos fueron muy similares y presentaron tres pares de cromosomas con constricción secundaria. Los resultados apoyan la propuesta de Sousa y Rudd de incluir al grupo de especies con $2n = 28$ en el género *Styphnolobium*.

## Abstract

In this study chromosome numbers ($2n$) and karyotypes of *Sophora secundiflora*, *S. velutina* var. *zimbabweensis*, *S. tomentosa*, *Styphnolobium japonicum*, *S. parviflorum*, *S. protantherum*, *S. burseroides*, and *S. conzattii* were determined. The first three species presented $2n = 18$, with a basic chromosome number of $x = 9$. These species had small variations in their karyotypes and one chromosome pair with secondary constriction. The other five species presented $2n = 28$, $x = 14$ and their karyotypes were very similar, three pairs showing secondary constrictions. These results agree with Sousa and Rudd's proposal to include species with $2n = 28$ in the genus *Styphnolobium*.

El género *Sophora* L. pertenece a la familia Leguminosae (= Fabaceae) y a la tribu Sophoreae. Se encuentra distribuido en las regiones tropicales y templadas de ambos hemisferios, y es un género grande y variable. Rudd (1972) señala que ciertas especies podían tratarse en géneros diferentes. Polhill (1981) señala entre 45 a 50 especies para el género, Rudd (1968) señala 75, mientras que Yakovlev (1967) enlista 40.

Rudd (1968) coloca a *Styphnolobium* Schott en sinonimia bajo *Sophora*. A *Styphnolobium*, sin embargo, se le ha dado reconocimiento como categoría infragenérica, así Yakovlev (1964) y Rudd (1972) lo reconocen como sección en el género. Hasta hace poco sólo se había hecho la transferencia a *Styphnolobium* de *Sophora japonica* y *S. affinis* y recientemente Sousa y Rudd (en Sousa, 1990) hacen lo propio con *Sophora conzattii* y describen una nueva especie para Nicaragua: *Styphnolobium caudatum*.

Entre 1981 y 1984 personal del Herbario Nacional de México (MEXU) colectó ejemplares aún no registrados para la ciencia y cuyas características hacían pensar en plantas pertenecientes al género *Sophora*. Comparando estas nuevas especies con material de *Sophora japonica*, *S. affinis*, y *S. conzattii*, Sousa & Rudd (1993), observan diferencias entre estas especies con especies del género *Sophora*, ubicando estos autores a las primeras en el género *Styphnolobium*.

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TABLA 1. Números cromosómicos ($2n$) y cariotipos de tres especies del género *Sophora* L. y cinco del género *Styphnolobium* Schott.

| Taxon | Localidad | Número cromosómico ($2n$) | Fórmula cariotípica | Constricción secundaria |
|---|---|---|---|---|
| *Sophora secundiflora* | México, Tamaulipas: Mpio. de Maquihuana, ej. La Peña, *Malda s.n.* México, Tamaulipas: Mpio. Bustamente, ej. Felipe Angeles, *Martínez s.n.* | 18 | 6m + 3m − sm | 1m |
| *Sophora velutina* var. *zimbabweensis* | Zimbabwe: semillas proporcionadas por el Herbario Nacional-Jardín Botánico de Zimbabwe | 18 | 6m + 3m − sm | 1m |
| *Sophora tomentosa* | México, Quintana Roo: Pto. Morelos, *Sousa 10995* | 18 | 4m + 4m − sm + 1sm | 1m − sm |
| *Styphnolobium japoicum* | Cultivada: semillas proporcionadas por el Jardín Botánico de la Universidad de Lisboa, Portugal | 28 | 13m + 1m − sm | 3m |
| *Styphnolobium parviflorum* | México, Veracruz: Mpio. Sn. Andres Tuxtla, *Ibarra s.n.* | 28 | 12m + 2m − sm | 3m |
| *Styphnolobium protantherum* | México, Jalisco: Mpio. La Huerta, Chamela, *Bullock 1495* | 28 | 11m + 3m − sm | 3m |
| *Styphnolobium burseroides* | México, Puebla: Mpio. Molcajac, *Sousa 11952, Sousa 11959* | 28 | 12m + 2m − sm | 3m |
| *Styphnolobium conzattii* | México, Oaxaca: Distrito de Pochutla, Cerro Espino, *Torres 4901* | 28 | 13m + 1m − m | 3m |

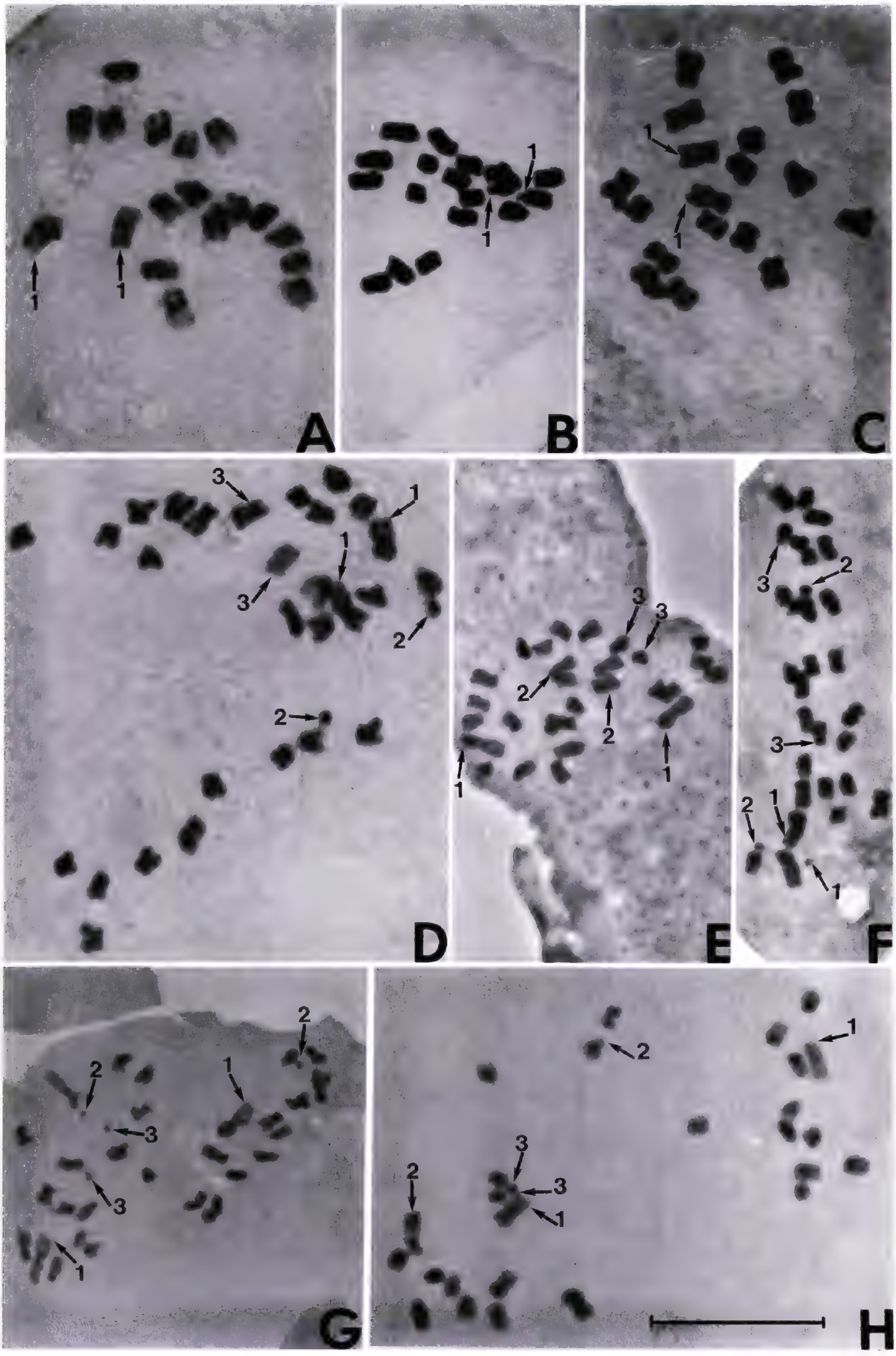
En un estudio palinológico de cuatro especies del género *Sophora* sensu stricto y seis del grupo *Styphnolobium*, Martínez (com. pers.) observó diferencias en relación a el tipo de retículo, tamaño y forma del grano de polen, estableciendo dos grupos. El primer grupo está formado por: *Sophora secundiflora*, *S. tomentosa*, *S. arizonica*, y *S. macrocarpa* y el segundo grupo está integrado por *Styphnolobium parviflorum*, *S. protantherum*, *S. burseroides*, y *S. conzattii*.

Revisando los estudios quimiotaxonómicos realizados por Izaddoost (1975, 1979) y Bailey (1974), se observa que *S. japonica* y *S. affinis* carecen de alcaloides (Izaddoost, 1975), ácido pipecólico y ácido 4-hidroxipipecólico (Izaddoost, 1979), a diferencia de las otras especies del género *Sophora* estudiadas por Izaddoost (1975, 1979). Además se aprecia que ambas especies contienen el polímero galactomanosa con composición similar (Anderson, 1949; Kooiman, 1971; Bailey, 1974), pero las demás especies del género *Sophora* estudiadas por Bailey (1974) no lo contienen. Reid & Meier (1970) y Bailey (1971), en base a sus investigaciones en la presencia o ausencia de galactomanosa en las semillas de leguminosas, suponen que estos compuestos pueden ser buenos indicadores genéricos. En relación al género *Sophora*, Bailey (1974) indica que aunque él sólo estudió ocho taxa en total, sus resultados parecen ser de considerable interés relativo a la revisión que hace Yakovlev (1967) del género, al colocar a *S. japonica* y *S. affinis* en el género *Styphnolobium*, ya que son las únicas especies que contienen galactomanosa.

Para las especies del género *Sophora* se han reportado números cromosómicos $n = 19$ y 11 y $2n = 16$, 18, 22, 28, y 36 (Federov, 1974; Goldblatt, 1981b, 1984, y 1988).

Goldblatt (1981a) consideró que la tribu Sophoreae tuvo un origen poliploide con $x = 14$, y posteriormente en su evolución ha habido una descendencia aneuploide con la diferenciación de líneas distintas en la tribu. Sólo se tiene conocimiento de $2n = 28$ para *Sophora japonica*, *S. affinis*, y *Cladrastis lutea* (Goldblatt, 1981a).

El objetivo de este trabajo fue obtener el número cromosómico $2n$ y el cariotipo de tres especies de *Sophora* pertenecientes a varias secciones y compararlas con el género *Styphnolobium* del cual se obtuvo información de cinco especies de las diez conocidas (ver Sousa & Rudd, 1993). Así se estudió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*Sophora secundiflora* [sección *Calia* (Berlandier) Rudd], *S. velutina* var. *zimbabweensis* [sección *Disemaea* (Lindl.) Yakovlev], y *S. tomentosa* (sección *Aigialodes* Rudd). En *Styphnolobium* se determinaron cariotipos para *Styphnolobium japonicum*, *S. conzattii*, y tres especies nuevas para la ciencia: *Styphnolobium parviflorum*, *S. protantherum*, y *S. burseroides* (Sousa & Rudd, 1993).

## Materiales y Metodos

Las plántulas y las semillas utilizadas en esta investigación fueron proporcionadas por el MEXU, Index Seminum del Jardín Botánico del Instituto de Biología UNAM y Herbario Nacional-Jardín Botánico Nacional de Zimbabwe, Africa (Tabla 1). Todo el material fue determinado por el último autor y los ejemplares de respaldo se depositaron en el MEXU.

Las semillas de las distintas especies fueron sometidas a tratamientos previos a la germinación. Las semillas de *Sophora secundiflora* (Everitt, 1983), *S. velutina*, y *Styphnolobium japonicum* germinaron al ser tratadas con ácido sulfúrico concentrado durante 5–15 minutos, las de *Sophora tomentosa* al remojarlas en agua destilada durante 48 horas y finalmente las de *Styphnolobium protantherum*, *S. burseroides*, y *S. conzattii* con escarificación mecánica. Después de estos tratamientos, se sembraron en cajas Petri con algodón y papel filtro esterilizadas y mantenidas en una estufa a una temperatura de 30 ± 2°C.

Las semillas que germinaron se colocaron en vermiculita para su enraizamiento, regándose con solución nutritiva Hoogland. Posteriormente las plántulas se transplantaron a tierra preparada en una proporción de tres partes de tierra negra por una de tierra de hoja, y actualmente se mantienen vivas en los invernaderos del Jardín Botánico. Para *Styphnolobium parviflorum* se obtuvieron plántulas traídas de la Estación Biológica de Los Tuxtlas, del Instituto de Biología de la UNAM, las cuales fueron mantenidas en los invernaderos del Jardín Botánico UNAM.

Los meristemos radiculares seleccionados para la observación de las células en metafase se obtuvieron de raíces secundarias en división celular activa. Estas raíces tenían una longitud de 1–2 cm y fueron cortadas de 7:30 a 8:00 A.M., pretratadas con el mitostático 8-hidroxiquinoleína a una concentración 0.002 M, durante cinco horas a una temperatura de 18°C y en la obscuridad.

Al término de este tiempo, las raíces fueron lavadas con agua destilada y después se fijaron en solución Farmer (alcohol absoluto y ácido acético glacial, en una proporción de 3:1); en seguida fueron almacenadas en el refrigerador a 4°C, donde pudieron conservarse por tiempo indefinido.

Para realizar la tinción de los cromosomas, las raíces se hidrolizaron con ácido clorhídrico 1 N a 60°C durante 10 minutos y posteriormente se introdujeron en una solución de Feulgen preparada a base de fúcsina básica de acuerdo con García (1988) durante una hora y a temperature ambiente.

El meristemo radicular ya teñido fue cortado y colocado en un portaobjetos limpio, agregando una gota de aceto-orceína al 2%. Después se colocó el cubreobjetos dándole un ligero aplastamiento y golpeándolo con la punta de un lápiz para separar las células y poder observarse al microscopio. Enseguida se fijó la preparación por el método del hielo seco (Conger & Fairchield, 1953) y finalmente se montaron los preparados en bálsamo de Canadá.

Para la elaboración de los cariotipos se seleccionaron 20 células de cada individuo, considerando cinco plantas por población. Las mejores células fueron fotografiadas en un fotomicroscopio III Zeiss, con un objetivo 100× y un optobar 1.25.

Los cromosomas de las células seleccionadas se dibujaron en una cámara lúcida Zeiss. A partir de estos dibujos y de las fotografías obtenidas se elaboraron los cariotipos. La clasificación de los cromosomas se realizó de acuerdo a Naranjo et al. (1986) basado en Levan et al. (1964).

## Resultados

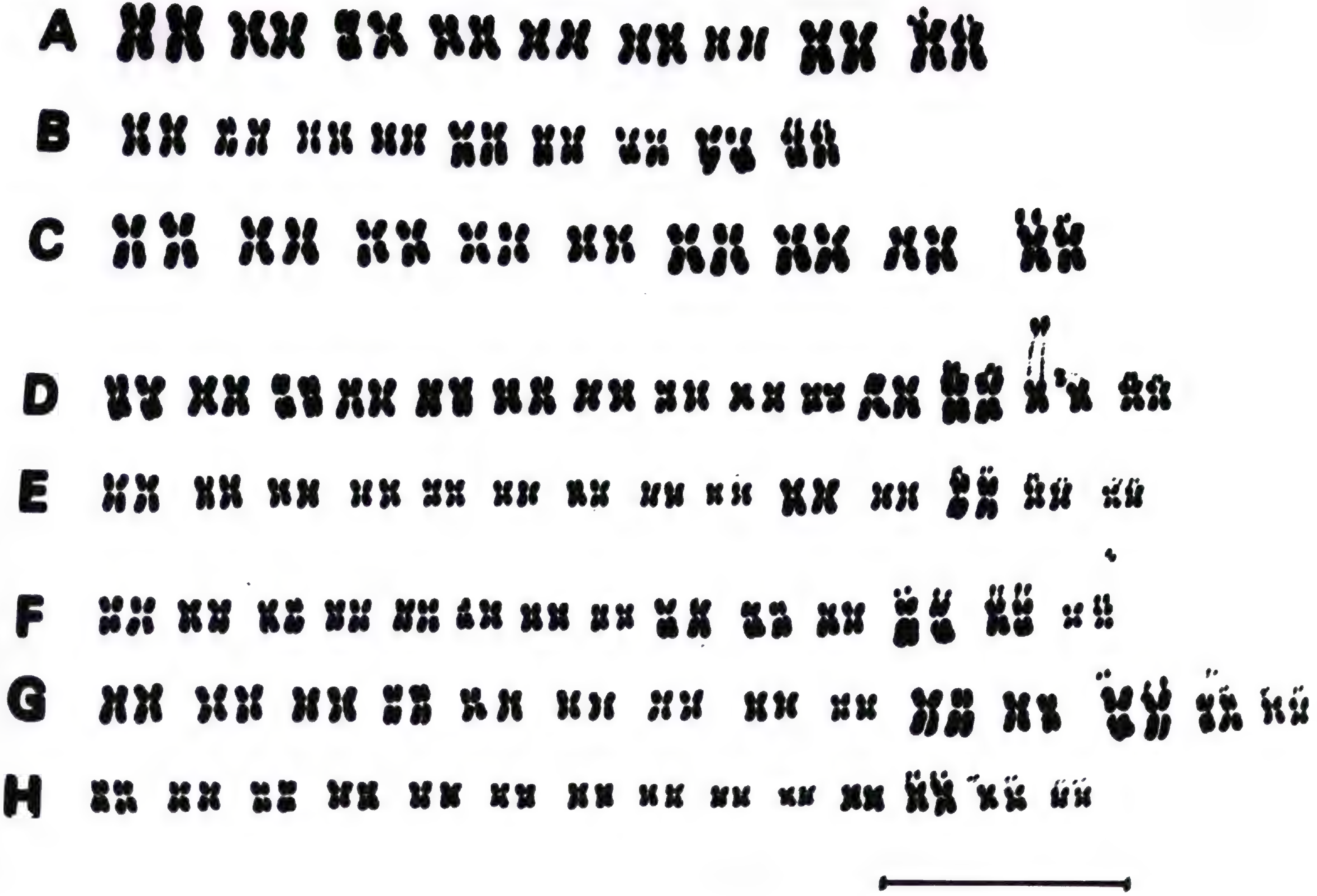
En la Tabla 1 y Figuras 1A–H y 2A–H, se indican los números cromosómicos ($2n$), las fórmulas cariotípicas, y los cromosomas con doble constricción de las ocho especies de los géneros *Sophora* y *Styphnolobium* analizadas.

## Discusion

En *Sophora secundiflora* se observó un $2n = 18$, el cual concuerda con los ya publicados por Atchison (1949), Darlington & Wylie (1955), y

←

Figura 1. Cromosomas somáticos de:—A. *Sophora secundiflora*.—B. *Sophora velutina* var. *zimbabweensis*.—C. *Sophora tomentosa*.—D. *Styphnolobium japonicum*.—E. *Styphnolobium parviflorum*.—F. *Styphnolobium protantherum*.—G. *Styphnolobium burseroides*.—H. *Styphnolobium conzattii*. Las flechas y los números 1, 2, y 3 indican los cromosomas con doble constricción. La escala corresponde a 5 μm.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Goldblatt (1981b, 1984). Un $2n = 18$ se determinó para *S. velutina* var. *zimbabweensis* y es la primera vez que este dato se informa, al igual que su cariotipo. El $2n = 18$ determinado para *S. tomentosa* en esta investigación confirma varios conteos previos informados para esta especie por Atchison (1951), Darlington & Wylie (1955), Federov (1974), y Goldblatt & Davidse (1977).

En *Styphnolobium japonicum* se observó un $2n = 28$, el cual está de acuerdo con los ya publicados por Darlington & Wylie (1955), Berger et al. (1958), Federov (1974), Fernandes et al. (1977), y Goldblatt (1981b, c, 1984). Para *S. parviflorum*, *S. protantherum*, *S. burseroides*, y *S. conzattii* se determinó por primera vez en este trabajo un $2n = 28$.

Sobre la base de los números cromosómicos de las ocho especies estudiadas, se encuentran dos grupos claramente definidos, un primer grupo con un número básico de $x = 9$ y un segundo grupo con un $x = 14$. El observar diferentes números básicos en especies relacionadas puede significar, según Löve & Löve (1974), que las mismas pertenecen a géneros distintos, siempre y cuando esta información se relacione con algunas características morfológicas (Moore, 1968), tal como ocurrió en *Hauya* y *Xylonagra* (Raven & Lewis, 1960). Esta situación es la presente en estos dos grupos de especies y los resultados citológicas son apoyados por los características morfológicas diferenciales mencionadas por Sousa & Rudd (1993), donde proponen la ubicación de las especies con $x = 14$ en el género *Styphnolobium*.

En *Sophora secundiflora* y *S. velutina* var. *zimbabweensis* se observó un cariotipo con seis pares de cromosomas metacéntricos y tres pares de cromosomos metacéntricos-submetacéntricos, un par de cromosomas metacéntricos en constricción secundaria. El cariotipo de *S. secundiflora* concuerda con el dibujo de los cromosomas de esta especie encontrado por Atchison (1949).

Kawakami (1930) reportó un $n = 9$ para *Sophora angustifolia* y el dibujo de los cromosomas de esta especie es semejante al cariotipo de *S. secundiflora* y *S. velutina* var. *zimbabweensis*. La única diferencia es que *S. angustifolia* no tiene un par de cromosomas con constricción secundaria.

Los cariotipos obtenidos para *Sophora secundiflora* y *S. velutina* var. *zimbabweensis* son ligeramente diferentes en relación a *S. tomentosa* en la proporción de metacéntricos, metacéntricos-submetacéntricos y submetacéntricos. Estas variaciones en los cariotipos pudieron haber sido causadas por inversiones pericéntricas y translocaciones desiguales (Stebbins, 1971).

Atchison (1949) obtiene para *Sophora tetraptera* y *S. microphylla* un $2n = 18$ y un par de cromosomas con constricción secundaria, concordande con lo que se encontró en las especies con un $2n = 18$ estudiadas en este trabajo.

Los cariotipos de *Styphnolobium japonicum*, *S. parviflorum*, *S. protantherum*, *S. burseroides*, y *S. conzattii* fueron muy parecidos, con tres pares de cromosomas metacéntricos con constricción secundaria. Se pudieron apreciar variaciones en la proporción de metacéntricos y metacéntricos-submetacéntricos, las que pudieron originarse por rearreglos cromosómicos llevados a cabo durante el proceso evolutivo de estas especies (Stebbins, 1971).

Las relaciones de brazos dentro de los cromosomas que comprenden el cariotipo son usualmente similares en poblaciones y especies relacionadas, así como el número básico de grupos de ligamiento génico (Kenton, 1986). Estas relaciones se mantienen en las especies analizadas en este estudio, el primer grupo con $x = 9$ y cariotipos similares entre sí, y son diferentes a las especies que muestran $x = 14$ donde los cariotipos de las cinco especies estudiadas son semejantes entre sí.

Considerando que la tribu Sophoreae probablemente tuvo un origen poliploide con un $x = 14$ y en su evolución posterior generó descendencia con números básicos menores, $x = 8, 9, 11$, por aneuploidías (Goldblatt, 1981a), se puede pensar que el género que se estableció primero fue *Styphnolobium* el que tiene un $x = 14$ y posteriormente por aneuploidías se estableció el género *Sophora* con un $x = 9$.

En base a los resultados obtenidos en este estudio se encontraron dos grupos citogenéticamente diferenciables, un primer grupo con un $x = 9$ y $2n = 18$ formado por: *Sophora secundiflora*, *S. velutina* var. *zimbabweensis*, y *S. tomentosa*, y un segundo grupo con un $x = 14$ y $2n = 28$ integrado

←

FIGURA 2. Cariotipos de tres especies del género *Sophora* L. y 5 especies del género *Styphnolobium* Schott.—A. *Sophora secundiflora* $2n = 18$, 6m + 3m − sm.—B. *Sophora velutina* var. *zimbabweensis* $2n = 18$, 6m + 3m − sm.—C. *Sophora tomentosa* $2n = 18$, 4m + 4m − sm + 1sm.—D. *Styphnolobium japonicum* $2n = 28$, 13m + 1m − sm.—E. *Styphnolobium parviflorum* $2n = 28$, 12m + 2m − sm.—F. *Styphnolobium protantherum* $2n = 28$, 11m + 3m − sm.—G. *Styphnolobium burseroides* $2n = 18$, 12m + 2m − sm. —H. *Styphnolobium conzattii* $2n = 28$, 13m + 1m − sm. La escala corresponde a 5 μm.

por: *Styphnolobium japonicum*, *S. parviflorum*, *S. protantherum*, *S. burseroides*, y *S. conzattii*.

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**Cover illustration.** *Pleurothyrium giganthum* van der Werff, by J. Myers.

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# Annals of the Missouri Botanical Garden 1993

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# KNOWLEDGE BROKERING: THE MECHANICS OF SYNTHESIS. INTRODUCTION[1]

*Nancy Morin*[2] *and*
*Theodore M. Barkley*[3]

Two items prompted us to propose this topic for the 38th Annual Systematics Symposium held at the Missouri Botanical Garden 4–5 October 1991. One is that scientific libraries have been growing rapidly, with the subsequent reduction in any one person's ability to remain current with his/her field. The other is that we systematists have an important element of synthesis in our work and are sensitive to the need to account for increasing amounts of information.

Systematists fall into two intergrading camps, monographers and students of the flora and fauna. The former study natural groups through a variety of techniques to provide new insights and to elucidate evolutionary relationships; the latter assess and synthesize information, particularly the works of monographers, and they prepare floras and manuals to account for all of the relevant organisms of a geographic region. These floras and manuals make the results of systematic research readily useable to a wider community, for they are a link between those who generate basic knowledge and the consumers of that knowledge. Floras and manuals are ever more important for wise stewardship as mankind becomes more obsessive at impacting the landscape. The Missouri Botanical Garden is engaged in several sizeable floristic projects, so it seemed appropriate to direct this symposium at the nature of information resources and their utilization.

A further factor in planning this symposium is the development of widely available computer capabilities for handling large amounts of information. We are the first generation of systematists to have the technical tools to evaluate the great amounts of information stored in our libraries and natural history collections.

The speakers were selected to present information and views of which systematists are not traditionally aware. We believe that we were fortunate to bring their unique expertise and breadth to this symposium.

The evening speaker, K. W. Bridges of the University of Hawaii, presented a dynamic, multimedia program that impressed those in attendance with innovative ways to consider information. Unfortunately, the program is not amenable to the printed page, and so it is not included here.

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[1] This and the six articles that follow it are the proceedings of the 38th Annual Systematics Symposium of the Missouri Botanical Garden, *Knowledge Brokering: The Mechanics of Synthesis*. The symposium was held 4–5 Oct. 1991 at the Missouri Botanical Garden in St. Louis, Missouri, U.S.A.

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# SYNTHESIS: A HISTORICAL PERSPECTIVE[1]

*Theodore M. Barkley*[2]

ABSTRACT

Biology and other scientific enterprises have generated an astonishing amount of information through the traditional techniques of experiment and observation. Little effort has been spent on the analysis or synthesis of the accumulated information, and there is both need and opportunity to do so. Some segment of future biologists must be trained in the emerging technologies for assessing literature and synthesizing information. The techniques of historiography may provide a model.

In 1955, I began graduate school, and in the course of events an advisory committee was formed, a thesis topic selected, the research methods agreed upon, and other routine matters were settled. Shortly thereafter, someone asked, "Have you exhausted all of the literature yet?" It was a perfectly reasonable question, and I set about finding and reading everything written on the topic. If difficult then, it would be all but impossible today. In the intervening years, the literature has "exploded," as they say, and access to it is both complex and incomplete. I cannot imagine asking a beginning graduate student in 1991 if he/she has exhausted the literature and then expecting an honest "yes" in response.

We all can agree that the enterprise of scientists has been productive, for libraries are bulging with the products of our efforts. The stunning success of the Soviets with their launch of the first space satellite, "Sputnik I," in 1957, prompted the U.S. government to increase greatly the amounts of federal support for basic research. Shortly after Sputnik I, generous support began for the whole spectrum of the sciences and technology, through the National Science Foundation, the National Institutes of Health, and various other agencies. We may be justly proud of our science, as we point to the libraries and note the long shelves of data and discussions and conclusions. However, we presume that the products of our science have a utility and significance greater than those we have been finding in them, if we could just synthesize the knowledge that is in hand.

## LITERATURE RESOURCES

The libraries of North American academic institutions are diverse; they were reviewed and ranked recently in the *Chronicle of Higher Education* (1991). There are a few giants, e.g., Harvard, University of California at Los Angeles and at Berkeley, University of Texas, and Yale, which have huge holdings and acquisitions programs. Harvard has nearly 12 million volumes and added 261,846 volumes in the academic year 1989–1990. Most of the major university libraries fall in the range of 1.5–3 million volumes and add about 40–60 thousand volumes per year. My home institution, Kansas State University (KSU), has a bit smaller library, with some 1.2 million volumes and an annual acquisition approaching 40,000 volumes. The KSU library has been growing at 4–6% per year, as have other academic libraries. The implication is clear. The KSU library is currently adding 564,000 inches of new shelf space (= 14,450 m) just to make the holdings accessible, and other libraries can tell of similar additions. The factors affecting the inescapable growth of libraries are treated by Okerson & Stibbs (1991) in a paper titled "The Library 'Doomsday Machine'." Librarians worry about budgetary problems and shelf space. The former can be handled, at least in theory, by appropriating more money; the latter is not so easy. The point is: How can we continue to store and access the accumulating literature?

We systematists are as committed to scribbling as anyone, and we have produced a wonderful trail of literature. Tod Stuessy (1990) has written a fine textbook on the topic, *Plant Taxonomy, the Systematic Evaluation of Comparative Data*, wherein he summarizes the practices and goals of taxonomy in its broadest sense, as seen by one of this generation's notable practitioners of the science.

[1] This paper is contribution No. 92-231-A from the Kansas Agricultural Experiment Station, Manhattan.
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It is a fine text for beginning graduate students to view the "state of the art," and it is deemed a worthy successor to *Principles of Angiosperm Taxonomy* by P. H. Davis & V. H. Heywood (1963). Both Stuessy and Davis & Heywood draw on wide bases of references, and both have extensive bibliographies.

Davis & Heywood is a tome of 532 pages, of which 44 pages are references, i.e., 8% or 1 page out of 12. Davis & Heywood cite 1,286 references, all published before 1963. On the other hand, Stuessy has 514 pages, of which 83 are references, i.e., 16% or 1 page out of 6. Stuessy cites 2,862 references, of which 1,919, or ⅔ of them, are from between 1970 and 1 July 1988 (the cut-off date in the preparation of the book), or a period of 18½ years. There are some interesting comparisons. Like his predecessors, Stuessy was selective. He gathered information and cited sources to illustrate how taxonomy is practiced, and he was not attempting to be comprehensive. Moreover, some authors and topics were given different degrees of importance by Stuessy than by his predecessors, e.g., H. J. Lam, a theoretician of floral structure, has one work cited by Stuessy and six cited by Davis & Heywood; I. W. Bailey, the comparative anatomist, has one work cited by Stuessy and ten cited by Davis & Heywood; H. G. Baker, the ecological systematist, has three works cited by Stuessy and thirteen cited by Davis & Heywood. Even when we allow for the differences in the predilections of the authors and the different times when they were writing, it is evident that a notable portion of what is published has a certain "shelf life," i.e., it is most relevant for a period of time after it is published, and eventually falls into respectable neglect. Note that the older literature is not wrong merely because it is old, rather, it is just politely forgotten. I wonder how often we have "reinvented the wheel" because of our inability to grasp what is hidden in the literature. E. S. Deevy, a geologist of Yale University, reviewed the relevant literature for his 1949 landmark paper "Biogeography of the Pleistocene," and even at that date he regarded the literature resources as "terrifying."

## Sources of Our Literature

The learning of antiquity has been admired by historians since the Renaissance, and much has been written about the great stores of information in the ancient world. The library at Alexandria surely was a justly fabled treasure of fact and philosophy. However, the literature from antiquity must be read with a different mindset than we moderns have, for books that were handwritten by scribes (rather than printed on a printing press) were written with the notion that they were merely permanent records and were not especially concerned with making a point, i.e., ancient books largely reflected conventional wisdom and were not polemics. Students of Hellenic scholarship note that Theophrastus wrote some rather obscure and elliptic sentences. Probably what has survived are his lecture notes; he had no idea that posterity would hang on his every written word.

The advent of printing from moveable type in the mid-1400s changed forever the ways we record and disseminate information. These changes and their impact are related most interestingly in *From Script to Print*, by H. J. Chaytor (1945). The author was a man of letters at Cambridge University, and he detailed how literate mankind of Europe was apprehensive about the impact of printing. Medieval schooling included a prodigious memory as a component, which printing later obviated. The ability to read had meant previously that a person could read aloud from manuscript texts. Printed books meant that the literate public would learn to read silently and rapidly, and books could be written to argue a case or to be read for personal entertainment. Chaytor was not aware of the irony in his book when he discussed the degradation of the medieval values of learning that were brought about by a new technology. Today, we are uneasy about the revolution of electronic information transfer, and we complain that kids spend too much time watching television. In 1500, people worried that the younger generation was getting hooked on reading.

About 50 years passed before the impact of printing and the realities of mass communication settled onto the literate communities of Europe. It happened nearly concurrently with the start of commercial exploitation of the New World, the rise of nationalism, and the great theological upheavals. Printing meant that Everyman could have a piece of learning and could write about it with the expectation that someone would read what he had written. Printing was essential to put learning into the public domain and, therefore, to the making of modern science.

Written publication was early done in books and in the Latin language of medieval scholarship. By the late 1600s, scientific publication was usually through journal articles in the colloquial languages. The development of scientific publication is detailed by Daniel Boorstin (1983) in *The Discoverers*. The shift of scientific pre-eminence from Italy to north-

western Europe through the 1600s saw, among other things, the rise of the Royal Society of London. Henry Oldenburg, a German who had immigrated to England, became the Secretary of the Royal Society and, in effect, was the general editor of publications. In this capacity, he designed the notion of the journal paper and initiated the *Philosophical Transactions*, which is the type specimen of the scientific journal. We here in St. Louis in 1991 should tip our hats in passing to Henry Oldenburg, for he was the most influential editor in the history of science.

Journals are published by scientific societies, commercial firms, governmental agencies, and rarely today but formerly even by individuals. Journals have two purposes: (1) to communicate information among those who are interested and (2) to record information (i.e., to communicate to later generations). I have no idea how many journals there are, or have been, in botany. Counting the entries in the B-P-H (*Botanico-Periodicum-Huntianum*) or in the *Union List of Serials*, used by librarians, would reveal many thousands.

## The Uses of the Literature

The advent of available modalities (e.g., inexpensive laboratory equipment, easy travel, relatively easy publication) moved the natural sciences from contemplative activity to increased observation and experiment. The 20th century has been the preeminent time for sophisticated observational and experimental methods. The graduate students of this century are trained with the presumption that good science means the addition of new data, derived from observation or experiment. Critical analyses and syntheses of previously published information have rarely been stressed in graduate training. Thus, review papers and state-of-the-art works have not been esteemed quite so highly as publications derived from fresh experiment and/or new observation.

Synthesis and interpretation of information already at hand, however, have always been a part of scholarship. Synthesizers may be recognized as four species, and like many species with which I am familiar, the boundaries among them are not sharp.

*1. Compilers and catalogers* write dictionaries, bibliographies, nomenclatural compendia, etc., with the goal of accounting for everything available on a particular topic. The approach and mindset of a dedicated compiler was described by K. M. Elisabeth Murray (1977) in *Caught in the Web of Words*, a biography of her grandfather, James Murray, whose passion was words and who organized and compiled the *Oxford English Dictionary*.

*2. Integraters* produce expanded catalogs that are edited to conform to a point of view, e.g., an encyclopedia that carries a particular view of mankind, or a regional or continental flora that implies a certain uniformity of taxonomic interpretation. Integration involves scientific judgment on the part of the integraters. A lucid but lengthy apologia for integration was presented by Jean Le Rond d'Alembert in 1751 as an introductory essay to the magnum opus of the French Philosophes, the *Encyclopédie* of Denis Diderot (d'Alembert, 1963).

*3. Digesters* selectively seek data and ideas from the literature and derive a comprehensive treatment to tell a story or instruct novices. Digesters write textbooks and state-of-the-art compendia. The aforementioned works of Stuessy and Davis & Heywood are examples of the works of digesters.

*4. Assimilators* are those who compile, integrate, and digest the works at hand. Assimilators produce expanded insights and new conceptual schemes. Among the great examples are the works of James Hutton and Charles Lyell, who assimilated the available information into the theory of Uniformitarianism and created modern historical geology. The Russian chemist D. Mendeleev likewise created the periodic table of the atoms through insightful assimilation. And so, too, with Charles Darwin and Alfred Russell Wallace, inter alia, who made the theory of evolution scientifically respectable. A notable current venture of assimilation in systematic botany is the preparation of a refined general system of classification to account for the present level of understanding in a justifiable phylogenetic scheme. Those engaged in this project include Armen Takhtajan (1980, 1991) in St. Petersburg, the late Arthur Cronquist (1981, 1988) in New York, and Robert Thorne (1976, 1983) in Claremont. Another contemporary assimilator of considerable influence is Lynn Margulis, who has developed the notion that the eukaryotic cell is derived from a prokaryotic ancestor that co-opted other prokaryotes, which, in turn, evolved into the intra-cellular organelles that are typical of the eukaryotes (Margulis, 1981). The elucidation of the genetic code rested upon some elegant experimental research, but the "central dogma" of molecular biology is an example of assimilation of data from disparate sources (Watson, 1968).

Some great works have elements of all four of these items, e.g., *Die natürlichen Pflanzenfamilien* of A. Engler & K. Prantl (1887–1915) is

largely an integration and digest of what was known, but the approach had an element of assimilation in that the editorial policy sought to use the work as a platform to support a particular understanding of plant evolution.

In recent years, our colleagues in ecology have found it necessary to synthesize their information into a whole that exceeds the sum of the parts, and they have done so by engaging mathematical concepts and computer technology. The resultant efforts are a subspecies of assimilation called "modelling," by which means it is hoped to create a precise depiction of the dynamics of the ecosystem or some part of it.

## A Model for Synthesis

Rather little is written on the methods of synthesizing great amounts of information, or at least little that is current among us biologists. Our colleagues the historians, however, might give us a clue from their methodology. Historians work on a subject for which there is neither experimental nor observational research, by our reckoning. Rather, historians are in the business of organizing and synthesizing diverse sorts of information about people, places, and events, and then composing possible conclusions. Historians note what has happened and then suggest interpretations as to how and why. Histories are written with different ends in mind, and distinctions among historical approaches are as old as written history. Herodotus,"the father of history," told the story of the Athenians' rebuff of the Persians so as to make it a timeless event of cosmic significance, but in the telling, he allowed inaccuracies of fact and some fanciful interpretations. Thucydides, on the other hand, recounted the Peloponnesian Wars with precise accuracy, but with no suggestion of a relevance that transcended the affairs of Greece. Needless to note, both historians have been read and respected through the ages.

The craft of writing history is called "historiography" and is often taught in history departments as a class for beginning graduate students. There are textbooks and workbooks in historiography, often with titles suggesting methods or techniques (e.g., Stoffle & Karter, 1979). Much effort is given to locating and evaluating sources of historical information, and some effort to the matter of integration of information. Historiographers usually assume an "angle" or a point of view about what is being studied, e.g., a Marxist historian could interpret the Reformation as a struggle among the social classes, whereas a theological worldview would offer a different explanation of events. Alteration of the point of view is termed "revisionism" by historians.

We biologists already share some procedures with historians, for we draw up hypotheses and test them, and we have our own ideologies and methods that are subject to re-evaluation. The point, however, is that historiographers have made a profession of learning to compile and evaluate information from the written record, and we biologists may certainly look to our colleagues in history for guidance and methodologies.

## A Modest Proposal

The time has clearly come to seek the "Broader Synthesis" from the information that is accumulating in the libraries. Most of us are established as practitioners in our professions; we are biologists or librarians or information manipulators, etc., and it is unlikely that many of us are seeking new avenues for our lives. However, please consider the following:

1. As noted earlier, we biologists believe that the products of our research have a value that transcends the miserly accumulation of facts in a library, i.e., our research collectively "means something." We do not often ask to whom it means something, or how it is meaningful. We simply assume that our research is part of a grander scheme, if we could but make the connections. By extension, the proverbial "answer to cancer" is likely to be elucidated by a synthesizer of information sitting at a computer terminal, rather than by a wet-bench researcher.

2. We are the first generation to see the opportunities of widely available electronic syntheses of information. The advent of printing changed the ways we handled information, and now the advent of inexpensive computer technology is assuring new and profound changes in the handling of information.

3. The techniques and mindsets of compilation and synthesis are hardly new—historians have been compiling and synthesizing for centuries.

Thus, we have the motive, the means, and the opportunity to tackle the treasure trove of information in our libraries. I propose:

Let us prepare a new subspecies of biologist, whose primary domain is not the field or laboratory (we have done *very well* at training field-and-lab researchers), but rather whose activity is mining the data in hand, and who is versed in the techniques of historiography as well as the approaches of traditional, observational, and experimental bi-

ology. The new biologist would not be a "historian," i.e., not a student of the history of science, but rather a biologist who addresses the Big Picture, asking new questions and testing hypotheses with the abundant and diverse information in hand. Think of the kinds of topics that such biologists could address, e.g., (a) changes in the structures of the biotic communities of North America since the melting of the Wisconsin ice sheet, (b) the impact of vegetation dynamics on air pollution and climate change, (c) an integration of paleobotanical evidence into the general system of angiosperm taxonomy.

Approaching these synthetic studies would require being well versed in all of the resources, plus having linguistic ability in more than English. Likewise, our newly trained synthesizer would require competence in electronic data management, where, I am told, the capabilities of the hardware far exceed the uses to which it is presently put.

Can we train a generation of biologists to regard the libraries as their sources of information? We will surely do so. But how long will we still have stick-in-the-muds, who assume that measuring a plant in the field or pouring from a test tube in the lab is worth more than asking new questions of data already in hand?

As we plan for our new subspecies of biologists, we would do well to co-opt the librarians early in the scheming. I imagine that they should be prepared for an eager group of biologists who have recently discovered The Library and who will treat it as we now treat our laboratories.

What will make Synthetic Biology a viable field for the future? Certainly two things: (1) some tangible resources to entice academia to engage these people and (2) thoughtful consciousness-raising among biologists to convince our colleagues that The Time Has Come. But the ultimate and compelling reason to study the accumulated body of information is simply because we have built it, and it is there.

## Note

Charles Darwin, Herodotus, James Hutton, Charles Lyell, D. Mendeleev, Thucydides, and Alfred Russel Wallace are noted in the text, but specific citations are not given here. All are historical figures, whose works are widely available, and for whom the abundant secondary literature is most accessible. The connections among Darwin, Hutton, Lyell, and Wallace are well noted by Eiseley (1958).

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# THE FUTURE OF SCIENTIFIC COMMUNICATIONS: MORE QUESTIONS THAN ANSWERS[1]

*Arlene E. Luchsinger*[2]

ABSTRACT

The paradigm of scientific literature has been the paper journal for the past 300 years. An economical design is needed for future information acquisition and storage, and the electronic journal may be the model for the future. Four issues seem to drive the production and dissemination of future scientific literature: the development of an acceptable standardized format; the copyright of intellectual property; the use and preservation of the literature; and funding for access to the literature. Today's electronic journals are characterized as being from the not-for-profit sector, originating with faculty members in universities. They are text only, they are not expensive, and they are relatively unknown. Electronic publishing will not supplant paper journals in the near future, but we are in the early stages of electronic communication.

For more than 300 years, scientific journals have been the medium for communicating new ideas and a stable means to chronicle scientific achievement. Before the first journal, correspondence to other intellectuals provided a method to distribute speculations, theories, and philosophies. The exchange of these letters was encouraged by the formation of official scientific academies, and the letters were read to the members who attended the meetings. The secretary of the society often assumed the role of soliciting, receiving, and responding to the letters of the correspondents. The secretary was also responsible for advising those who could not attend the meetings. The monotonous hand copying of the news and ideas for each of the absent correspondents was laborious and time-consuming (Kronick, 1976).

The printing press, Gutenberg's contribution in the mid-15th century, was one of the greatest innovations of history. The printing press had been most successful in producing books and was used in 1665 to produce the first scientific journal, the *Philosophical Transactions* of the Royal Society of London. As scholarly correspondence increased, the character of the scientific journal changed to include original research, reviews of research, book reviews, and news reports. The letters have continued as letters to the editor (Chappell, 1970; Kronick, 1976).

From ancient clay tablets to manuscripts to printed books and journals, microforms, and computer files, libraries over the centuries have obtained, preserved, and organized these sources of information. Before the end of this century, another format will be common in most libraries: information of an electronic design.

Library subscriptions to journals involve a commitment to continue their purchase and preservation on an annual basis. Debate and concern has been growing over the escalating cost of scientific journals and the increasing number of new journals. This expansion of journal literature has provided not only more titles than ever before, but more specialized titles in every discipline. The proliferation of journals (the number doubles every 10 to 15 years) and the shrinking acquisitions budgets of most academic libraries will force the focus of academic libraries from acquiring resources for teaching and research to providing access to information (Broad, 1988; Smith, 1991).

Librarians need to make decisions about how to utilize their resources. Should they acquire paper copies of the information, or provide access to information using electronic means? Will the ability to access other collections be more expensive than continuing to subscribe to the paper copies? Will libraries rely on cooperative borrowing, or shift to purchasing journal articles from commercial

[1] Discussions with William Gray Potter contributed to my understanding of and interest in this evolving field. I thank my colleague, Virginia Benjamin, who read the manuscript and made helpful comments.

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sources? Several commercial providers exist now, and more are projecting entry into the marketplace (Jackson, 1992; Lenzini & Shaw, 1992). What level of staff interface will be needed for the various modes of access? The cost for delivery of an article may depend on the urgency of the requestor and the mode of delivery. That is, articles may be sent by mail, overnight courier, electronic mail, or fax. Who will decide whether a library user needs information immediately or if documents can be delivered after a brief wait by conventional interlibrary loan? Some librarians believe that the institutions that can provide ready access to necessary materials will recruit the brightest faculty and students; those that cannot provide this access will lose the competitive edge (Mitchell & Saunders, 1991).

Four issues seem to be driving the production and dissemination of future scientific literature: format, the copyright of intellectual property, how the literature is used and preserved, and funding for the access to the literature.

## New Approach to Packaging Information

The current paradigm of scientific literature is the paper journal. To change this paradigm, we must approach the current publication dilemmas with innovative mental restructuring, fresh approaches, and renewed imaginations. Because one impetus for change is the increasing cost of paper journals, the change to electronic formats will not happen if the costs are more than the users are willing to pay.

Electronic publishing may be defined as publishing that encompasses all computer-assisted methods for the production, manipulation, and dissemination of information (Brailsford & Beach, 1989). Electronic publishing encompasses on-demand publishing, bibliographic databases, desktop publishing, documents on optical disks, etc., but the electronic scientific journal is a major concern to the academic community. What is the future of the electronic journal? What are the technical problems of production? What are the implications for libraries? How will access to the electronic journal be provided?

The characteristics of today's electronic journal are outlined by Okerson (1990). These journals are from the not-for-profit sector; they originate with faculty members in universities; they are text only; they are free or inexpensive; they have generous copying statements; the circulation or subscription lists are rapidly growing; and they are relatively unknown. A recent publication, *Directory of Electronic Journals and Newsletters* (Strangelove & Kovacs, 1991), lists 30 journals and more than 60 newsletters that are available over electronic networks.

More typical of electronic information implementations are electronic indexes such as *Biological Abstracts* and *Agricola*, which correspond to their paper counterparts. Most college and university libraries have or are planning an on-line catalog of their holdings with author, title, subject, and keyword searching (Burke, 1991; Sitts, 1988). Some libraries have installed journal indexes such as *Medline* and *Current Contents* that are accessed through the on-line catalog. These electronic on-line indexes are available not only to users in the library but also to remote users through dial-up access. On-line journals exist now that are versions of the same title published in paper. The American Chemical Society in the early 1980s made its primary journals available on-line. They are accessible through the on-line database service, STN. Electronic journals could conceivably be archived on a mainframe computer and linked to on-line catalogs.

Rather than subscribing to an entire journal, a profile of a consumer's subject interest could be matched electronically against articles in a wide range of journals. Much more information would be made available than if one subscribed only to those journals that could be supported financially; the cost would be for the articles that were selected. The consumer could be the individual scientist, or a library that serves a scientific community (Lancaster, 1989).

There are some obstacles to the use of electronic media or formats. Illustrations are not a part of current electronic communications. Many scientists lack or do not want to use electronic communications. The medium may appear to be difficult and inaccessible. Most people are accustomed to a paper format for journals, and paper products are readily available through conventional and uncomplicated means (Loken et al., 1991; Okerson, 1990).

Standards are lacking for the format used to convey electronic data. These standards include, but are not limited to, the coding for specific instructions to the computer such as what designates underlining, italics, or paragraph spacing. Standards are absent for encoding and distributing texts and accompanying images. Standardization of symbols and graphics and the rules for their use must

be developed, and there must be interfaces for text and images (Gould & Pearce, 1991; Weber, 1990).

The problem of moving textual material among different types of computers with incompatible operating systems and differing applications software was solved by the American Standard Code for Information Interchange (ASCII). ASCII is a binary code used in all personal computers. However, ASCII lacks the codes for such things as editorial and critical comments, book formatting instructions, printer commands, and other features that add worth to the idea of electronic publications. ASCII text files prevent the use of different fonts such as foreign character sets, mathematical symbols and scientific notation, illustrations, and color. There are other text files that might solve the problem, but may not be practical for users who do not have the necessary software to use those files (Bailey, 1991; Basch, 1991; Kaufman & LeClercq, 1990).

Today's scientific paper publications have high-quality color illustrations. We do not know the limitations of monitor and printer displays, but to be successful, microcomputer hardware must be inexpensive and improved so that the quality of the data reception on screens and printers is high and is as acceptable as paper copy (Bailey, 1991; Weber, 1990).

Another challenge is the establishment of high-speed research networks and their integration into a national networking infrastructure. These networks must have the speed and bandwidth to accommodate an increasing data transmission requirement.

Legislation to establish the National Research and Education Network (NREN) was first introduced by Senator Albert Gore, Jr., in 1988. Each year since then, revised versions of this act have been introduced in both the U.S. House and Senate. The proposal is to connect supercomputer centers and to accommodate the massive amounts of data produced by high-performance computer projects. NREN would expand and improve the existing interconnected group of research networks such as NSFNET, MIDNET, and SURANET that are collectively known as Internet. It is expected to be completed by the year 2000. Federal agencies will be expected to work with state and local agencies, libraries, educational institutions, and private network services to provide access to electronic information resources held by publishers, research facilities, and libraries. The creation of the NREN will expedite the publication of electronic journals (Henderson, 1991; Brownrigg, 1990).

## Copyright

With the invention of the photocopier came the concern that these machines would put some journals out of business. The photocopier removed a section of readers who might have subscribed to a journal if that was the only way they could have acquired the papers they needed. The publishers normally do not receive revenue from these readers (Brailsford & Beach, 1989).

Copyright is not intended as a permanent monopoly, but software vendors have been known to use technical strategies to thwart attempts to copy a program into a user's computer memory (Pool, 1985).

Photocopies may be made of today's paper journals and mailed to a colleague or borrowing library. Fax machines may be used to transport that same copy faster. An article in digital form may be sent from a computer workstation and arrive at one or more distant workstations almost instantaneously. What will keep the receivers of the document from redistributing the material (Weber, 1990)?

Sharing or even reselling books has never been prohibited, and such prohibition would not be enforceable. Colleagues may read information from your computer terminal or ask for a copy of a copyrighted electronic publication you have ordered, paid for, read, and stored in your computer's memory. It is easy to do this; press a couple of keys, and the information is sent to an electronic mailbox. If you comply, you may be disregarding the copyright laws (Pool, 1985; Solomon, 1985).

Enforcement of copyright laws from the commercial publisher's view is an economic, not an intellectual, issue. If copyright cannot be enforced, that is, if the reader does not have to pay to read an electronic document, there would be little incentive for a commercial publisher to distribute merchandise in an electronic format. Will publishers permit storage of their electronic publications in a central site? If copyright is not necessary for commercial publishers to collect revenues, and if a charge is collected for each use of the electronic publications, will copyright be obsolete (Smith, 1991)?

## Using and Preserving Electronic Literature

According to Dillon (1991), scholarly journals are read for several reasons: for work purposes, to keep up with the literature, for reference, or for learning. Her study indicated that readers of academic journals scanned the tables of contents first,

and then rapidly browsed and turned pages quickly back and forth through an article. Electronic versions must have the capability to scroll through pages as well as skip forward and backward through a document. Users of electronic journals will want to perform tasks other than full reading of a text. Paper is more adaptable than a video screen; the white paper and black ink format will not transfer easily to screens.

There is a rush by the scientific community to get information into print. Today the lag time between submitting a paper and seeing it in print is usually from 4 to 18 months. Full-text electronic journals could be printed in any location and forwarded to users, thus dramatically shortening the time lag.

Informal use of electronic mail (e-mail) systems is increasing in academia (Loken et al., 1991; Smith, 1991). Ideas are exchanged, but this communication form has met resistance when it threatens the more formal channels, that is, the refereed journal (Piternick, 1989). The role of the scientific journal today is to provide a mechanism to notify others of the results of research. Publishing is also done for scholarly prestige and the academic reward system. Will electronic publications be acceptable for promotion, tenure, academic honors, author recognition, and increases in salary? If articles published in peer-reviewed electronic journals are not accepted for promotion or tenure, will researchers be kept from fully exploring the possibility of publication in the format? Who will be on the editorial board—only those who are skilled enough to handle the manipulation of electronic text? Will the part of the publication process that is not automated be the editorial work by referees and editors? Will the contributions of scientists who are uneasy about the integrity of scientific data be jeopardized (Eisner, 1991; Gould & Pearce, 1991; Smith, 1991)?

Invasion of privacy may be an issue if publishers of the electronic information systems collect data about subscribers' proprietary interests and sell this information to a third party. Some publishers today sell the subscription lists of their paper publications.

Haywood (1988) described the "electronic aristocracy." They consume, enjoy, and digest electronic information in private without having to share with others. They work in an information-rich environment and can afford the up-front connect and search charges, or they work for an organization that pays these charges. These users could also be termed the "information elite."

A significant portion of the world's population will be the "information poor." These people will not have access to electronic publications. This will be true not only of third-world scholars, but also those in some developed countries. Until language translation systems are available, English will continue to dominate the databases, and those who cannot read English will be "information poor." Inefficient communication and transportation networks, inadequate telephone and mailing services, and a dearth of technical expertise will challenge the development of electronic information delivery in the third world (Haywood, 1988).

Libraries subscribe to and maintain journals that only a few people read or consult when first published. Those journals, however, may build readership in later years as certain papers begin to be cited. Preservation of printed volumes, films, photographs, and slides has been a task of librarians. The paper format has been successful and has endured through the centuries. The librarians of the future dealing with electronic publications may not have the preservation problem—there simply may not be anything to save.

There are several nontrivial obstacles to the preserving of electronic data files. Magnetic media degenerate due to heat, sunlight, humidity, dryness, magnetism, dust, and unintentional erasure. How long will an electronic media exist without self-destructing? Data tapes, hard and floppy disks, and digital optical storage have a lifetime of a few decades (Kaufman & LeClercq, 1990). Who is and who will be doing the archiving of intellectual content of electronic publications?

Soon the technology of today may be obsolete. Will we be able to continuously move stored data from one technology to another? Electronic standards will be more important than ever. It will also be essential that archives of electronic serials be maintained by libraries or other organizations (Bailey, 1991).

## The Economics of Electronic Publishing

Information acquisition and publishing is becoming increasingly centralized. Users of inexpensive packages of information (e.g., books) should not be disenfranchised by the sudden disappearance of information if that information becomes accessible only by electronic means. Users must be able to access the electronic networks at a reasonable cost. Government funding will be needed to bring modern, fast, and relevant information networks to the majority of the population (Bailey, 1991; Haywood, 1988).

The level of university support for networked

publishing ventures is a concern. Endorsement by scholars and publishers is essential. A charge for use could accommodate those for-profit publishers. The noncommercial presses, such as universities and societies, might not be threatened as long as the editorial and review processes remain within their purview (Okerson, 1990; Smith, 1991). Most revenue will come from subscriptions, fees for connect time, royalties for viewing and printing pages, charges from users downloading information, and rental of compatible equipment. There will be less revenue, and nearly all of it will be delayed in coming because most use will be "on demand." Advertising income will be lost. Publishers worry about the revenues they will expend and what the profits will be. They need to know how to make money on this technology (Standera, 1987; Eisner, 1991).

The publishing process for scholarly print journals is financially underwritten by the scholarly community either from page charges or library subscriptions. Government grants may provide funding for the research for new data. This new information is forwarded to a journal publisher, and frequently grants provide the resources for page charges. State and federal governments provide the money for libraries to purchase the information that was formulated by the researchers.

Rogers & Hurt (1990) described a scenario for a Scholarly Communication System. Briefly, scholars could publish and read other publications on this electronic network. The system could also be used as a communication device to seek data from current and archival files. Those with valid passwords could leave signed statements related to the articles they have read in a comments field. An article that had been in the system for six months would be flagged for review. The author would have several weeks to use the responses from the comments section and prepare a final, revised version to submit to a review board. The boards would perform the reviews now undertaken by editors of scholarly journals. If the article was approved by the board, it would become a permanent part of the communication system.

Grants from the participating universities, foundations, and government agencies would provide the capital for establishing the system. Annual fees paid by each academic institution would pay for selection and training of reviewers, honoraria for reviewers, and administrative costs. Operation costs and hourly usage charges would be paid by a membership fee from each institution. Authors whose articles were printed out by the system would be provided with royalty payments. Libraries would have access to the system and could print files using sophisticated printers (Rogers & Hurt, 1990).

This new communication system would provide numerous advantages to colleges and universities. The amount of money spent for subscriptions to publications would be significantly decreased. The need for additional library space would be reduced. The hours spent by library personnel processing, shelving, and reshelving journals could be better spent on helping users find the information they want. The system would establish and enforce the format standards to be used for storing information. Universities would regain control over the review and publication of research. That is, rather than having publishers and their referees decide who gets published, the universities would have a role in choosing the members of review and management boards. The system thus could provide better information for universities to make hiring, promotion, tenure, and salary decisions. In addition universities would regain copyright control (Okerson, 1991; Rogers & Hurt, 1990).

## One Society's Vision

In 1988 the president of the American Physical Society (APS) formed a six-person Task Force on Electronic Information Systems. The extensive report of the Task Force was published in the *Bulletin of the American Physical Society* (Loken et al., 1991). While the report concerns the physics community, the findings and visions may apply to all disciplines.

Some of the findings were: (1) those who have otherwise avoided the use of computers for research are utilizing word-processing on desktop personal computers; (2) many have personal computers that are linked to electronic services and on-line databases; (3) the use of electronic mail (e-mail) through BITNET or Internet has increased in frequency and scope; and (4) e-mail is used for short communications, nonlocal collaborations, and submission of papers (Loken et al., 1991).

The APS vision is for the year 2020, but it may be reached by 2010 or even 2000. Workstations with color-graphic resolution comparable with today's best on-paper printing may be used by the majority of scientists. These workstations may be connected and have access to local or remote servers within seconds. A single, worldwide, fiber-optic network with a structure that is analogous to a highway system with superhighways, state and regional highways, local roads, and driveways is planned. Storage of information will be $10^{-4}$ less

than the cost of storing documents on paper. Software standards will be in place to deal with text, equations, graphics, illustrations, and multimedia output (Loken et al., 1991).

Computerized scientific literature delivered to graphic terminals may have output that is three-dimensional, dynamic, and that can be viewed in arbitrary orientation, with arbitrary magnification, and at variable speeds—all selected by the individual viewer. The user may be able to request documents, sections of documents, or texts to which the original document refers. The user may be able to make comments on the document. The capacity of computers to perform translation of natural languages will be developed. This will permit an author to submit a paper in one language and have it read in the languages of the readers' choice. Authors may submit their manuscripts by electronic submission to publishers using a form that follows an international standard. Messages between referees and editors and between editors and authors may be electronic (Loken et al., 1991).

The APS Task Force felt that there could be separate databases supporting broad subjects. The individual databases could form a central database that would be accessible. Managers of the databases would be responsible for the physical operations such as maintaining the hardware, software, and networking, as well as making and implementing the policy decisions of the supporting organization. This organization could be a government or private enterprise (Loken et al., 1991).

Search strategies will be efficient and easy to use. Entire documents may be indexed by bibliographic information, descriptors, symbols, and perhaps diagrams. Searches will be more interactive; computers will be used as expert systems to lead an investigator through a search. Today, the results of on-line searches are downloaded to paper or floppy diskette. In 2020, downloading will be over the network into computer files (Loken et al., 1991).

Most scientists have a set group of journals they read and use as vehicles for publishing their papers. What impact will the electronic publication and retrieval of documents have on the journal in which it is published? Will journals as we know them exist? Today, many scientific journals are only sold to libraries. The cost to the libraries is the same whether the journal has a large or small readership. In 2020, the use of the electronic publication could be monitored. These observations could be used to determine the number, kind, and extent of any use (Loken et al., 1991).

## Conclusion

Print journals will probably continue as the primary method of scholarly communication in the near future. However, we are in the beginning stages of the development of electronic communication. Paper will not disappear, and the new media will not threaten the future of the printed book. Electronic journals may be read on-line, but most scientists will want a printed copy. Publishing in both print and electronic formats may be necessary, and this will increase the cost to the publisher. Long-term storage will be in electronic formats rather than microfilm and microfiche.

The promise of successful technology alone will not force the acceptance of electronic publishing. The real concerns may be fiscal, legal, regulatory, social, and political factors rather than technological issues. However, as computer technology becomes a central force in scientific dialogue, electronic publishing may supplant the printing press as a comparable force in communication among readers.

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# OWNERSHIP AND OUTREACH: A MODEL FOR ADMINISTRATION OF SHARED DATA

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ABSTRACT

Sharing data is a common practice among researchers in all fields. In most, however, sharing is limited to data passed among a few researchers known to each other. In this paper, issues raised by larger scale, multiple use of data are discussed. The two major issues that arise are ownership of data and access to data generated by others. Ownership is both a legal and a behavioral issue, as yet unresolved. Even without clear consensus on ownership, however, means for promoting multiple use of data that accommodate researchers' concerns can be found. Access issues include which data should be retained, the costs associated with retention and maintenance, and how access to others' data is managed. The Utah Resource for Genetic and Epidemiologic Research (RGE) has developed from a committee of data contributors and data users into a program for management of multiple-use data. Examination of its history and operations gives some insight into how issues of ownership can be managed. From that example, five general components of a multiple-use data management system are generated. Finally, throughout the paper an argument is made for institutional consideration of data management issues at the policy level prior to development of formal data sharing mechanisms.

The concept of multiple-use data in scientific research is not a new one; in fact, sharing data is common among researchers. However, the context of sharing data for most researchers is that of Researcher A sending a data disk or a copy of lab results to Researcher B. This form of data sharing appears to raise no eyebrows within our current research culture. It is when a larger scale is proposed that support for the concept of shared, multiple-use data falters. At that point, promotion of data sharing seems to run into some perceptual roadblocks that, if not addressed, will continue to impede the development of multiple-use data on a large scale. The evolution of the Utah Resource for Genetic and Epidemiologic Research (RGE) has included the development of a certain focus, albeit fuzzy, to the apprehensions that the idea of multiple use of data generally raises. It is my purpose here to delineate the issues involved and then use the experience of RGE to demonstrate how those apprehensions may be addressed. That in turn will serve as the basis from which to generate a model for management of effective data sharing.

I begin with two caveats: first, as the experience of RGE is solely with human subjects data, the issues raised and the model outlined will at times be unique to research with human subjects. However, many of the principles involved should be applicable to other areas of biological research. Second, in the interests of simplicity, I use the following definition of data, which summarizes the lack of consensus on a single definition among researchers and administrators considering data sharing: Data are whatever the researcher designates as such (derived from remarks, U.S. Public Health Service, 1990).

## OWNERSHIP

Perhaps the pivotal concern raised in any discussion of data sharing is that of data ownership. Who owns the data generated in the course of scientific research? As demonstrated by the results of a workshop on "Data Management in Biomedical Research" convened by the Public Health Service in April 1990, consensus on this issue does not exist. Investigators who have generated data in their research regard those data as "theirs." The PHS stated that "When PHS awards a research grant, the data developed by the grantee institution are owned by the grantee institution . . . ." Institutions that receive grants and support investigators (many of whom wrote the grant proposals in the first place) are caught in the middle.

Ownership, in a legal sense, deals with property and one's rights to use of that property. Ownership

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is important, as Fishbein (1991) pointed out, because ". . . whoever owns also controls dissemination, especially the timing of dissemination, publication and proprietary rights. Moreover, whoever owns data also has the ultimate ability to control their preservation and destruction." Basing her argument about data ownership on the principle of "works-for-hire," Fishbein agrees with the position taken by the Public Health Service that institutions are the owners of data generated in the course of federally supported research. It is her assertion that "this basic principle regarding ownership of data is [not] open to debate as a legal matter." In her opinion, the problems raised by the question of ownership are, in fact, ethical problems of appropriate conduct, rather than legal ones.

In legal terms, the Public Health Service and Fishbein are correct about ownership of data. I differ, however, with Fishbein on the roots of the actual issues with which we deal. Issues of what is, or is not, ethical conduct in the sciences are secondary consequences of the important aspect of human behavior just noted: scientists who have generated data regard them as "theirs." It may be a logical argument that, since most university policies and procedures manuals exempt certain products of scholarly work from university ownership, those products not exempted are indeed owned by the university. Viewing the exempted scholarly works from another perspective, however, a different logic appears.

The book or article or review is owned by the author, who generated it. On this, we all can agree. Moving backward, the book or article or review is usually based on data generated by the author.

If the product is owned by the person who generated it, how can it be that some of the pieces of the product, generated by the same person, are not "owned" by that person also? In behavioral terms, although not perhaps in strictly legal terms, data and product seem inextricably intertwined. Ownership of one appears to confer ownership of the other. Any resolution of the issue of ownership must accommodate this perspective.

## Ownership: Responsibility and Stewardship

Resolution of this disagreement between human and legal realities will take many forms. The concept of stewardship mentioned by Fishbein is one that maximizes the utility of the data, while minimizing friction over ownership. No matter who owns data in a strict legal sense, all parties benefit from appropriate management of those data. In policies regarding data being developed at the University of Utah, it is proposed that a fundamental relationship to data be that of responsibility. Differing parties in the university community have differing responsibilities to each other and to the data generated there. As examples: The university has a responsibility to protect the research interests of all members of its community. To do so, it may be necessary to require that an investigator who moves to another university take responsibility to ensure that data generated by his/her team are available to all members of the original research team. Or: For a researcher to enjoy the benefit of the university's responsibility to deal appropriately with allegations of research misconduct, the researcher must take responsibility to maintain data in a form that facilitates resolution of those allegations. Focus on the various responsibilities for data acknowledges their value for both individual and collaborative work and encourages productive use of data while protecting the interests of all parties. Final resolution of the issues of ownership will probably occur with the evolution of the scientific culture. During that process, however, specific institutional policies regarding data provide mechanisms by which work can proceed without undue constraint. However, as noted in the 1989 Institute of Medicine report, "The Responsible Conduct of Research in the Health Sciences," "few academic institutions have established explicit standards for responsible research practices . . . ." Without such policies, Fishbein's conclusion that ". . . if the academy does not come to a consensus—preferably in some formal way—about the ethical and professional obligations of researchers in stewardship of their research data, the courts or the government may do it for them" is unfortunately logical and predictable.

## Access

The other major category of concerns usually raised about data sharing is access. In order for data to be shared (that is, used by someone other than the generating researcher) they must be retained, maintained and accessible. The volume of research data, enormous in the biomedical arena alone, limits the feasibility of this. Even in large, well-funded programs that rely on sharing of data, such as the Human Genome Project, problems of size and access have arisen (Aldous, 1991). We will have to make some difficult decisions as to which data are kept for shared use. Prospective utility of data will have to be evaluated relative to the costs of retention, maintenance, and accessi-

bility, preferably on an institutional level, so that resources may be allocated in the most effective manner. What is effective will vary from institution to institution, and from one college or department to another within a given institution. If we wish to encourage sharing of data, problems associated with retention, maintenance, and accessability must be identified so that practical solutions can be found.

### Access: Retention

Which data justify retention? At the 1990 PHS data management workshop, substantial agreement was reached on retention of certain types of data. The first type of data were those that were expensive to generate. Epidemiological data were cited in this category, as were data from longitudinal studies. The sheer scale of most such research makes the data generated very expensive. Making such data available for multiple use reduces the cost of future work in those areas, as well as in areas not yet foreseen. The second kind of data to be retained were those that are no longer replicable (or that would be extremely difficult to replicate). The major example noted here was studies on species that are no longer available for research purposes. The final category of data to be kept, and the one for which there was much less agreement than the above two, was data that had significant public policy implications. Keeping these data ensures that the foundations of the policies are as open to review as the policies themselves. Within a given institution, other types of data may be deemed worthy of retention; these are mentioned here only as examples of some data retention recommendations.

The benefits of retaining certain data for multiple use can be agreed upon. There are, however, other factors in the decision to make data available for multiple use. Chief among these are the costs of retaining/maintaining the data and costs associated with providing access to them.

### Access: Storage Costs

The first set of costs associated with data sharing are those incurred in storing data. Data may be stored as hard copy (such as lab notebooks, X-rays, photographs, printouts) or electronically. Either form of storage entails space costs. Space, on computers or in filing cabinets, is a valuable commodity in most institutions. Its costs may be onetime, such as purchase of filing cabinets, or ongoing, as in monthly charges for electronic data storage. In the case of most epidemiological data, for example, size is a significant factor in space calculations. Furthermore, how data are stored may be a factor in accessibility. For example, data on a tape in archives are not as accessible as data present online and may thus not be as valuable to another researcher. Minimizing storage costs may also minimize utility, thus subverting the purpose of storing the data.

### Access: Confidentiality

A second element in decisions about the cost of some data retention is confidentiality. Maintenance of human subjects data requires strict protections for the privacy of the subjects and the data about them. Locking file cabinets, appropriate computer security procedures, and staff training in appropriate data handling methods are necessary. Personnel and personnel training are necessary appropriate maintenance of confidential data. Costs are both onetime and ongoing.

### Access: Cataloging Costs

Another major factor in the costs of maintaining data for multiple use is cataloging. A prospective data user needs to know exactly what the data are, where they reside, in what format they are available, and what the access procedures are. While oversight by the generating researcher is absolutely necessary to the cataloging process, creation and upkeep of data descriptions is not an appropriate use of researchers' time. Personnel becomes a significant cost determinant here.

### Access: Management

The final area of questions raised about access is who will have access to the data and for what purposes. At this point, the human logic about ownership is significant. Researchers have concerns about what others will do with "their" data. Will it be used to further scientific inquiry or perhaps for purposes of discrediting the generating researcher? Will it be used to do work the researcher has planned to do? Will it be used in research that is not sound? These are legitimate concerns. Allowing the generating researcher to control access to his/her data resolves them. However, requiring a scientist to manage use of the types of data identified as valuable for multiple use would add an intolerable burden of administrative work. Appropriate management of access requires development and administration of mechanisms that allow reasonable control by generating researchers yet promote maximum use by others. As in retention/maintenance, costs here are associated with personnel and the media in which data are stored.

Costs of data retention, maintenance and access for multiple use clearly exceed the capacity of single researchers or even of most research groups. Thus, in order to promote data sharing in the biological sciences, the costs must be accepted on an institutional level. RGE is an example of one such institutionally supported data sharing program.

## History of RGE

RGE is a data administration program supported at the University of Utah. Its primary responsibility is a large electronic database of records on past and present residents of the state, which is used in genetic, epidemiologic, and demographic research. It began the the mid-1970s when University of Utah researchers interested in genetic epidemiology obtained family history records from the Genealogical Society of Utah and received permission from the Church of Jesus Christ of Latter-Day Saints (LDS or Mormon) to compile family history records (three-generation genealogies) into a computerized genealogical database. At the same time, the growing group of researchers began to computerize death certificates from the Utah Department of Health and cancer records from the Utah Cancer Registry. Both of those data sets, along with the 1880 U.S. census of Utah, were linked to the genealogical records. By the early 1980s, research uses of these data were extremely varied: cancer epidemiology, historical demography, cancer genetics, genetics of autism, epidemiological research into the effects of nuclear fallout, and genetics of early coronary disease were the major areas of research. The management needs occasioned by the diversity of research projects using an aggregate of private, public and research data were the impetus behind the creation of RGE.

## RGE Operations

Perhaps the single most important facet of RGE is that it functions as an intermediary between data contributors and data users. RGE "owns" neither data nor research. Data contributors own their data and negotiate agreements with RGE regarding how those data may be used. Data users own their research projects and work with RGE to complete projects within the constraints of the data agreements. RGE has custody of the data and the responsibility to ensure that the agreements are upheld.

With this structure, many of the ownership issues that impede data sharing fade from importance. Dissemination and publication, issues of ownership identified by Fishbein, are but insignificantly different from other research practices. While publications using RGE-held data are reviewed, the reviews are limited to ensuring that certain agreed-upon protocols are used. Control over preservation and/or destruction of new information (data) created by the data user is retained by the user. Control over preservation and/or destruction of data created by the data contributor is, as defined in the agreements described above, retained by the contributor.

The issue of the constraints on the use of data placed by the data contributor is a more thorny one. Where data ownership is absolutely clear, as with the LDS Church family history records, the data contributor may impose whatever restraints on usage desired. Publicly held records, such as those from the Utah Health Department, are subject to state law and regulation, with which few would argue. Our experience with data generated solely by researchers and then given to RGE custody is limited. That limited experience leads me to propose, however, that if agreement can be reached on the need for retention of certain data, agreement can be reached on appropriate use, as well as on protections for the data contributor. However, such agreements are considerably easier to reach if the institution has already defined its policies regarding management of data. In those circumstances, the outlines of a culture of multiple-use data have already been traced.

The data within RGE's custody fit the criteria for retention described above—they are data that would be very difficult and expensive to duplicate. Support for storage and maintenance of these data includes an administrator, a database manager, and a dedicated computer with both hardware and software support. User fees are charged and used to augment institutional support. Past experience has shown that reliance solely on research grants, without providing a "floor" of institutional support, allows data to deteriorate. The funding fluctuations inherent to American research grants result in support that can be insufficient to maintain data quality, particularly over time. In addition, without institutional support, institutional memory about the data can easily be lost. In both cases, the utility of the data diminishes.

Confidentiality of data and management of access are the responsibilities of the RGE administrator. Confidentiality protections are central to the access procedures; both electronic and personnel protection measures must be defined. Extensive guidelines about use requirements are provided to all researchers prior to application for access. Before access to data is granted, a research protocol specifying confidentiality protections must be ap-

proved. All users must sign confidentiality pledges accepting their responsibility to protect the confidentiality of the data. These protocols are required in addition to the more general protocols required by Institutional Review Boards. IRB approval is required for any projects requiring access to individually identifying information.

Applications for access are reviewed by a committee that includes representatives of data contributors, computer personnel, and other scientists in the field. The review is not a peer review of the proposed science, but a review of the procedures for management of confidentiality and specific data. As most users are familiar with the data and the procedures, the review is not a tortuous process. The RGE administrator is responsible for working with prospective users to acquaint them sufficiently with the procedures so that reviews proceed smoothly. The data manager also works with prospective users to ensure that proposals that are submitted can be accomplished with RGE-held data.

## Components of a Multiple-Use Data Management Program

Over the past decade or so, RGE has developed to provide a group of users with a shared data management program. Although the user group is not large, it is diverse. Applying RGE's experience to the apprehensions outlined earlier gives a picture of a multiple-use data management system grounded in the following components:

1. Some characteristic of the data makes them valuable yet not easily available elsewhere.
2. Ownership is managed in such a way as to protect the interests of all parties. Written agreements, review authority, and appeal proceedings are integral parts of the system.
3. Detailed guidelines, procedures, etc., are developed by data contributors and data users in concert. These are provided to any researcher prior to application, along with consultation with staff who are familiar with the data and the guidelines.
4. Administration is handled by a non-research third party, whose function is defined as accommodating the constraints of data contributors while promoting scientific use of the data.
5. An adequate "floor" of support is guaranteed so that data do not deteriorate, information about the data is retained and available, and there is sufficient staff support to data contributors and data users.

While development of a multiple-use data management program will likely proceed more smoothly in an institution with already defined data management policies and practices, such definition is not a requirement in the creation of a data sharing program.

## Summary

The particular constellation into which these components are grouped will be determined by the data, its contributors, users and research environment. RGE is one such constellation that works at the University of Utah. Evolving from the specific to the general, operation of RGE has served as a basis from which institutional policies regarding data are being developed at Utah. Creating a locally effective constellation of the above components will proceed more smoothly if such policies are developed prior to designing any shared data management program. The combination of institutional data policies and a well-designed data management program provides a strong basis for the promotion of sharing of data in the biological sciences.

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# EMERGING TECHNOLOGY FOR BIOLOGICAL DATA COLLECTION AND ANALYSIS[1]

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ABSTRACT

Increasing concern for Earth's biological resources—their inventory, protection, and use—has prompted efforts to modernize practices and procedures for botanical data collection, storage, and retrieval. America's Global Change Research Program, the International Geosphere/Biosphere Program, the International Space Year, and related multinational efforts are already requiring massive species databases and analyses of plant species information, much of which is either not readily available, or locked in herbaria on specimen sheets. One of the first orders of business for botanists and taxonomists should be to explore new and emerging technologies that can reduce the time, expense, and human resource requirements for automating existing herbarium data, optimizing field data collection, and analyzing massive, computerized biophysical data sets. A few of these prospects are described here in context of my research on the flora of the Rocky Mountains.

It is estimated that Earth's flora and fauna represent somewhere between 10 and 30 million lifeforms, of which a scant 1.7 million have been named scientifically (Wilson, 1989). Human impact on the global environment is rapidly altering and destroying whole ecosystems, and untold numbers of species are becoming extinct before they have been discovered, named, and assessed for their beneficial properties. There is an on-going demand to complete a worldwide species inventory, but this cannot be realized without using new and emerging technologies. In the early 1980s it was hoped that new computer technology would permit scientists access to data and images from herbarium specimens, allowing them to compare and identify the large number of new collections being made. Our vision of what that technology can do for botanical and taxonomic research has vastly broadened as the technology has become more sophisticated and more generally available.

In this report, I review the potential for new taxonomic data collection and processing techniques, ranging from electronic notepads and microminiature, digitally compatible cameras to database development and management systems applicable to herbarium inventories and research laboratories. For example, an on-line image database that permitted botanists to retrieve pictures of type specimens, rotate them in 3-D, and zoom in on key structural elements would significantly reduce the time and personnel required to manage herbarium collections. Field camps and herbaria equipped with a portable imaging system could communicate with a centralized image database to compare specimens located in other collections, or to those freshly collected in the field. Finally, the availability of interactive databases designed for specimen attributes, landscape analysis, and human imprints contributing to landscape changes would permit a new genre of research hypotheses and modeling. Already in the 1990s, significant strides have been made in imaging, database management, telecommunications, miniaturization, global positioning, and computing technology that will allow rapid modernization in field and herbarium practices. Moreover, there are major new capabilities evolving in the general tool kit of Earth-observing technologies that will enhance not only the collection of taxonomic, ecophysiological, and distributional data about species, but will also reduce the time and expense of analyzing the data and disseminating the information.

The Rocky Mountains represent an exciting regional laboratory for adopting new data collection and management technology for plant species information, and will be used here to illustrate the potential. The origin and development of the Rocky Mountain flora throughout the Tertiary Period, the shifting and sifting of elements and communities during the glacial Quaternary Period, and the manifest changes and imprints superimposed by human cultural systems in the past millennium (especially in the past half-century) all contribute to our understanding of the area as an ancient but constantly

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changing and increasingly vulnerable set of environments. The region stretches for more than 25° latitude, from northern New Mexico to the Laird River in British Columbia, and rises at its highest peaks to over 4,000 m from a general elevational base of 1,600 m.

## Rocky Mountain Data Sets

Activities are underway that enhance the Rockies as a technological test bed. The Flora of North America (FNA) Project (Morin et al., 1989), the revision of the *Flora of the Rocky Mountains*, the Greater Yellowstone Ecosystems Project, and the Global Environmental Monitoring System/Global Resources Information Database (GEMS/GRID) are all efforts aimed at the development of plant species databases. Likewise, they have all shown a compelling need to address global change issues on a regional basis.

The FNA project will result in a 13-volume synoptic flora of the plants of North America and a computerized database derived from this information. In one design (Morin & Tomlinson, 1988), 13 data files were envisioned: taxonomic placement, scientific and vernacular name(s), authorities, synonyms, type specimen(s), literature, morphology, breeding system(s), chromosome numbers, flowering time, elevation, habitat, and distribution. At the Floristics for the 21st Century workshop (Morin et al., 1989) it became clear that the database would also need to contain an image file, data on relative abundance or rarity, status as threatened or endangered, economic significance, plant–animal associations, ethnobotanical uses, and accurate locality data. Such data sets, when merged with other biophysical parameters, define a geographic information system. In sum, the data universe should consist of both taxon data and spectral/spatial data from satellite and/or aircraft remote sensors, and geographic information systems (GIS). These data sets need not be co-housed, but they must be accessible through networks, and their files must be compatible to address management questions being raised by environmentalists and global change scientists.

The revision of the *Flora of the Rocky Mountains* began in earnest in 1989, spearheaded by Ronald L. Hartman, curator of the Rocky Mountain herbarium at the University of Wyoming. The chapter describing the origin and development of the flora of the Rocky Mountains (Morain, in review) to be included in this publication contains a section on human impacts since European settlement. It is in this context that the development of a species information system compatible with a GIS seems most urgent. Habitat fragmentation (and outright loss of some habitats), environmental changes induced by acid rain and the rise in concentration of greenhouse gases, fire management practices, economic activities (both extractive and recreational), and alterations due to plant introductions are all human imprints that affect the pace and direction of floristic and vegetational change. Today, only a few areas of pristine wilderness remain in the Rocky Mountains in an expanse of logged, mined, grazed, and farmed land. There is an extensive network of national forests, national parks, state forests, wilderness areas, national monuments, and other "protected" or multiple-use areas, but even these suffer from overuse and general environmental degradation. The species they harbor already represent isolated, and in some cases peripheral, populations about which we know very little. Worse, the boundaries on these civil and political units become evident on the landscape as economic development and land use changes outside the units evolve, thus fragmenting any avenues for plant migration that may someday be necessary.

The Greater Yellowstone Ecosystem has emerged in these concerns as a specific area of interest. The range of local climates, elevations, lithologies, and soils results in a natural fragmentation of the landscape and striking vegetation dynamics. It is the largest ecosystem remaining in the Rockies that has been relatively untouched, and as a consequence there are many questions about the ecosystem that should be addressed on behalf of the region's general history and development. There are disjunct elements of California, Great Basin, and boreal vegetation that contribute to the ecosystem's uniqueness. It has long been recognized that management questions of such intricacy require joint and collaborative research and the use of modern technologies to coordinate the programs of many state and federal agencies. The Greater Yellowstone Ecosystem Coalition is a step in that direction. Agencies meet periodically with the Nature Conservancy to discuss problems within the National Park area and to coordinate their various management programs. A geographic information system is being created to catalog and explain the interactions between plant and animal species, especially the rare or endangered forms stranded by their environmental history.

The United Nations Environment Programme (UNEP) has established a Global Environmental Monitoring System (GEMS) as a means for assessing environmental conditions, the quality of life,

and the changing conditions of life around the world. The United Nations Environment Programme GEMS/GRID database has been developed to assist these efforts. As of 1990, GRID consisted of some 15 global data sets (such as soil, topography, climate, vegetation) representing the first-order physical environmental parameters affecting human welfare. They are largely compiled from sets created at national and smaller scales, but private sector efforts are also gaining importance, as are those contributed by institutional (e.g., environmental, university, and other not-for-profit) groups. At the national and regional levels, mission-oriented government agencies have contributed a wide array of information coverages. What is clear, however, is that many GRID coverages are at too coarse a resolution for regional application. Their utility is greatest at continental, hemispherical, and global scales. Nevertheless, they provide a stimulus for refinement and the basis for initial model building. A companion effort, focused on the Rocky Mountains, is the Land Cover Pilot Project undertaken through the International Geosphere/Biosphere Program (IGBP), which is designed to collect transect data across the region.

## Global Change Modeling

Global change modeling will impact the course of research in the Rocky Mountains and could serve as a driver for modernizing taxonomic data collection. Morain (1990) has summarized the main arguments. If the concentration of $CO_2$ and other greenhouse gases doubles by the middle of the 21st century, some climate models show that by the mid-2000s the Earth's temperature could rise between 1.5°C and 4.5°C (UNEP/GEMS, 1987). A 3°C increase would emulate the global temperature of 13 million years ago (Mathews, 1987), roughly analogous to the Middle Miocene. While the actual rate, cause, and magnitude of increase is debatable, it is generally agreed that there will be an increase, and that as a result, there will be northward and altitudinal redistributions of species, plant communities, and whole vegetational zones toward cooler regimes.

Concomitant with global warming, a change in precipitation regimes up to 5% is predicted by climate models (Mathews, 1987). Some areas would gain, while others would become more xeric. Several models suggest that there would be a decrease in total annual precipitation in the Rockies. Clearly, the flora will respond to these temperature and moisture stimuli differently. Predictive modeling and visualization based on a modern species information database, and an environmentally oriented image-based GIS that contains detailed ecophysiological data on a species-by-species basis, will be required to: (1) know which new assemblages could possibly populate habitats of the future; (2) predict how long it would take them to adjust by natural means; and (3) determine whether there is sufficient land area at higher elevations to sustain them.

At present, there is almost no evidence by which to assess the rates and directions of biotic adjustment in the Rocky Mountains, but we do know that existing communities and distributions are in disequilibrium with today's environments (Habeck, 1987). Becker (1961) suggested that the Oligocene Florissant flora of Colorado expanded into Montana at a rate of 1 m every 30 years. If the anticipated rate of global warming actually occurs, some studies have suggested that vegetation in the Rockies will have to migrate 300 km poleward, which at Becker's rate would take 9 million years, or hundreds of meters upslope (perhaps as many as 500). Although many species of plants might possess the ecophysiological tolerance to adjust to these migrations, others with slower rates of migration, or those that lack access to new habitats will either require human intervention to ensure the introduction of suitable genetic stocks into new localities or they will necessarily become rare, endangered, or regionally extinct. In any case, the need to migrate upslope will be ecologically impossible for alpine tundra forms, and may be very restrictive to numerous other species, since land area will physically diminish. As Lewin (1989) indicated, the depth of biological knowledge required to manipulate species' geography is extraordinarily complex. But such manipulation will undoubtedly be required because natural migrations will be stymied by existing and evolving land use restrictions. To achieve this in-depth knowledge will require analysis using GIS technology, an ability to model changes through time, and to then animate the rates and directions of predicted change for better long-term planning.

## Mechanics of Synthesis

Existing data sets are so diverse in their origin and structures that a prerequisite exists to assemble and convert these assets into a body of regional data. The compatibility of GIS databases operating in a multitude of computer hardware/software configurations is essential if economy of operation is to be achieved and duplication avoided.

In addition to the GEMS/GRID coverages that are available in both raster and vector format, there

are several databases under development at the federal level. NPFLORA is a module in the National Park Service database called COMMON (G. Waggoner, pers. comm.). It contains almost 80,000 records on some 14,300 taxa in the National Park system, including 12 areas in the Rocky Mountains. Although the module is not specimen based, it is a documented floristic list of species present in each of the park areas. It currently contains information to the subspecies level including regional distribution, status, habitat descriptors, and citations. It will soon include synonyms as set forth in the National List of Scientific Plant Names (NLSPL) prepared by the U.S. Department of Agriculture–SCS (Soil Conservation Service, 1982).

Yellowstone National Park has been developing a GIS for management purposes. At present, the system consists of two vegetation layers: habitat types, as defined by Daubenmire (1966); and cover types, as defined by dominant emergents. In addition, there are coverages (some only partial for the 2.2 million acres) for bedrock geology, precipitation, and hydrology. Digital line graph (DLG) and elevation models (DEM) are also included. The system is running on a Masscomp computer using Earth Resources Laboratory Analysis (ELAS) and Geographic Resources Analysis and Statistical System (GRASS) software and operates in both raster and vector modes. NPFLORA is available for Yellowstone but has not yet been merged into the GIS. A specimen-based electronic catalog is also being created by the Park museum curators, but its relation to the Yellowstone GIS has not been addressed.

There are several other databases under construction, or already operating, for management areas within the Rockies. Many of these are housed in universities or federal agencies (e.g., DEM and DLG files) and contain coverages captured for different reasons. For example, the Technology Application Center (TAC) at the University of New Mexico is compiling a checklist of Rocky Mountain species, as developed by John T. Kartesz at the University of North Carolina. This represents the first time that a modern checklist has been constructed for the region and from which we can research the phytogeography of species. In a companion effort the TAC team is retrieving the lists of rare and endangered species from the Nature Conservancy's Heritage Programs in each state for each of the mountain ranges within the Rockies. We are plotting these data onto 1 : 250,000 scale maps and loading the results into ELAS image processing software to create a region-wide database. The data are then plotted onto Digital Elevation Models and will eventually be superimposed onto NOAA Advanced Very High Resolution Radiometer and Landsat Thematic Mapper (TM) data.

## Enabling Technologies

As the elements of an initial operating system are being configured, it clearly will be necessary to develop the means for rapid and efficient species data collection in the field, and for rapid information retrieval and dissemination in herbaria. Among the obvious candidates for this modernization are global positioning systems (GPS), pen-equipped computers, microminiature cameras, new satellite data collection systems, and advanced visualization technology.

### Global Positioning Systems

Global positioning system (GPS) technology, like GIS, has already reached commercial status and has numerous technical and scientific applications. Compact and low-cost, hand-held GPS devices are already available. Magellan Systems Corporation, for example, has produced a battery-powered unit called the NAV1000 PRO, which weighs only 0.85 kg and measures 21.5 × 9.0 × 5.0 cm. It has an operating temperature between −40°C and 70°C and operates on six AA alkaline batteries. It provides two-dimensional, single-fix, autonomous positioning accuracies of 25 m, or three-dimensional accuracies of 30 m in 2.5–3 minutes. Using two receivers, accuracies improve to 5 m in 2-D, and 10 m in 3-D. Data can be downloaded directly into a data logger or personal computer. Its display is a 4-line, 16-character alphanumeric liquid crystal display (LCD).

Gilman et al. (1989) have also described a hand-held system, called TRIMPACK, that has been designed to address applications where the GPS equipment must function independently of external power, mechanical support, or antenna. By using LCD technology, they keep power consumption under 3 watts and capture 20 hours of continuous use. Industry leaders are expecting the price per unit to decrease rapidly from about $3,000 to perhaps $500. Other references on hand-held GPS technology include McDonald (1989), Smith et al. (1989), Baker (1987), and Smith (1985).

Regarding taxonomic data collection specifically, Wilkie (1989) has described his use of a portable GPS in the Ituri rainforest of Zaire. He used a 12-volt gel cell battery-powered Magnavox 4400 backpack receiver with a detachable 0.6 m aluminum antenna. The system was solar-recharged with an ARCO G100 solar panel. With it, he was

able to obtain 3 hours of receiver time per recharge, during which he captured three-dimensional geographic locations in forest openings as small as 0.125 ha.

Hand-held GPS technology represents an essential link in creating a species information system for the Rocky Mountains. When in place, the full complement of 21 NAVSTAR satellites will permit continuous data collection in remote areas, thus freeing taxonomists from interpolating or, worse, guessing at the location of their collection sites. Environmental attributes such as aspect and elevation will also be much more accurate and consistent, especially if field crews are correlating data from several receivers.

## PEN-EQUIPPED COMPUTERS

An exciting new development in computing is the pen-equipped electronic clipboard. This genre of devices is expected by the industry to sweep the marketplace for applications where traditional clipboards are already used to record data. One company, Grid Systems, has produced a 2-kg "Gridpad" containing the power of a hand-held (not laptop) personal computer. It looks essentially like an "etch-a-sketch" tablet, but one that derives its electronic utility from recognizing block characters and storing them in battery-backed RAM cards. It quickly recognizes characters in nine different languages and has a "fill-in-the-blanks" graphics form that could be ideal for recording specimen data in the field. Gridpad is a DOS machine, but other manufacturers are planning to use ROM-based DOS and Windows environments. An essential ingredient in this evolving capability, of course, is to ensure that data are transferrable to office PCs and workstations—the objective being to avoid data reentry and transcribing errors. Pen-equipped technology is so new, and potentially so large, that several American and Japanese manufacturers have entered the market and are currently posturing for software companies to develop applications.

In an article titled "Computers Without Keys," Normile & Johnson (1989) described Canon's "Ai Note" and Sony's "PalmTop." These, too, use an electronic pen to allow users to take notes, do word processing, calculate printed formulas, and create graphics. The PalmTop is 21 × 16 × 5 cm with a 10 × 15 cm LCD display, and weighs 1.5 kg (battery included). It uses a 68HC000 microprocessor and has 2MB ROM for programs and 320KB RAM for temporary data storage.

In support of modernizing field taxonomy, now is the time to ensure that adequately robust pen-equipped computers and software are developed for botanists' needs. Those elements in the design of the global species information system that require accurate field data could form the basis for the requisite software, and could even include 2-dimensional or 3-dimensional positional data obtained from hand-held GPS observations. For management of herbarium specimen data, an ability to hand-scan information quickly and download it simultaneously into a database is essential.

## MICROMINIATURE CAMERAS

A new generation of video imaging cameras is available for field and herbarium use. These are described in product literature as microminiature color charge-coupled device (CCD) cameras that record images in digital format. The cameras are about the size of a person's thumb, the imaging element of which is about one-half inch consisting of as many as 420,000 CCD sensing elements. Together with their accessories, these cameras could be ideal tools for recording field specimens using power from a field vehicle (current technology would permit ranging distances up to 30 m from the vehicle), or in converting herbarium specimens to CD-ROM formats. Resolution of these systems also permits close-range imaging of plant morphologies. Among the other specifications attractive to field and laboratory taxonomy are: (1) electronic shutter speeds ranging from 1/60th to 1/10,000th of a second; (2) low (10 lux) subject illumination requirements; (3) wide range of operating temperatures (−10°C to 40°C); (4) 12-volt DC or 120-volt AC power source; and (5) an array of interchangeable lenses from 3 mm to 24 mm.

## SATELLITE DATA COLLECTION SYSTEMS

The Earth Observing System (EOS) is a major element in the National Aeronautics and Space Administration's "Mission to Planet Earth," but it is also a major international cooperative element in the International Geosphere/Biosphere Program, the U.S. Global Change Research Program, and the World Climate Research Program (Morain, 1991; Thompson, 1991). It has a profound potential for impacting the ways and means for collecting, storing, disseminating, and analyzing biological data of the future. Currently it is designed as a 15-year program to commence with a series of EOS-A satellites in 1998. Its three primary components include a Space Measurement System (EOSSMS), consisting of a wide variety of sensors; the Data and Information System (EOSDIS), designed to archive and disseminate data, and to

supply products to the science and research communities; and the Scientific Research Program (EOSSRP) consisting of institutionally supported individuals and collective research efforts.

*Space Measurement System (EOSSMS)*

The needs of the Earth-observing and Earth System Science research communities encompass the ionosphere, atmosphere, hydrosphere, lithosphere, and biosphere. Past and present satellites are already collecting data from these realms using imaging and nonimaging (sounding and profiling) systems, and many of these data sets will be readied for general access as part of a pre-EOS dissemination system. The EOSSMS sensors are divided into two categories representing a plethora of experiments and applications in the earth sciences. The first category consists of facility instruments, so called because they represent the core NASA instruments for EOS, and will be managed mainly by NASA facilities or other closely related non-NASA laboratories. The second category is referred to as Principal Investigator Instruments because they represent more narrowly defined, special purpose experiments. Data captured by both sets of instruments will be divided into three categories to ensure their widest use and analysis: (1) facility investigations; (2) principal investigator investigations; and (3) interdisciplinary investigations.

Each of the facility sensors has numerous measurement and integration functions as well as scientific applications. The Moderate Resolution Imaging Spectrometer (MODIS), for example, will be collecting data for at least two dozen experiments, including: (1) the dynamics of snow and ice over large areas; (2) studies of primary production in the world's oceans; (3) species variability and improved carbon and nitrogen cycling determinations; (4) monitoring global vegetation dynamics; (5) global aerosols monitoring; and (6) land surface temperature measurements. MODIS-N (nadir) will have 36 channels for data capture ranging from 0.4 to 14.2 $\mu$m in 10- to 360-nm bandwidths. MODIS-T (tilt) will have 32 channels between 0.4 and 0.88 $\mu$m in 10- to 15-nm bandwidths. Such fine resolution spectral data are expected to provide insights into ecosystem dynamics, global change research models, and general vegetation monitoring.

*Data and Information System (EOSDIS)*

EOSDIS represents the means by which data processing and analysis are to be made available to the scientific community. At the heart of all EOS activities is the EOS Operations Center located at Goddard Space Flight Center in Greenbelt, Maryland. It will serve as a communication link between EOSSMS and EOSDIS to ensure sensor operations and raw data capture. Working together with the System Management Center, the Instrument Control Facility, and the International Partner Operations Center, raw data and level-0 data will be distributed to a network of centers called Distributed Active Archive Centers (DAACs). Level-0 data will be released to these centers to be further refined by their internal Product Generation Systems into level 1 or higher products, or stored for later use in their Data Archive and Distribution Systems. This initial operating structure and management plan for EOSDIS is referred to as Version 0, because ultimately several versions will succeed this design. Version 0's focus is on science data processing, but is designed to be flexible and evolutionary as subsequent technologies, expertise, experience, and infrastructure come into play (Taylor et al., 1991).

An integral part of EOSDIS is represented by data that have been, and are now being, collected. These pre-EOS data sets are divided into a "Pathfinder" series having global extent (e.g., NOAA AVHRR/Global Area Coverage, Total Ozone Vertical Sounder, and Geostationary Operational Environmental Satellite—GOES); a "Precursor" series of important, but not necessarily global, data sets (e.g., NOAA AVHRR/Local Area Coverage, Airborne Visible and Infrared Imaging Spectrometer, and Thermal Infrared Multispectral Scanner); and "non-EOS" data (e.g., Landsat Thematic Mapper and Multispectral Scanner). The DAAC at EROS Data Center has recently inaugurated the Global Land Information System as a prototype in Version 0 to provide access to some of these data: namely, AVHRR, Landsat, 1-degree USGS Digital Elevation Models, Matthews Global Vegetation Data Set, and Major World Ecosystems, among others. These are accessible for searching, browsing, and interrogating through Internet and direct-dial using IBM-compatible terminals.

## ADVANCED VISUALIZATION TECHNOLOGY

Three-dimensional image processing technology and 3-dimensional GIS modeling techniques are in the forefront of new earth science applications, especially those in meteorology, oceanography, hydrology, and geology, where depth sounding and profiling have been long-term 2-dimensional tools. In terrain analysis, the availability of digital elevational models (DEMs) has enabled ecologists to

superimpose computer classified land cover types onto a static representation of relief, and to even quantify the elevational ranges, aspects, and total area occupied by each type. At a higher level of sophistication, and requiring massive computer processing, techniques are available for moving the terrain past an observer. Several videos have been produced by the Visualization Laboratory at the Jet Propulsion Laboratory in Pasadena, California, to illustrate how static terrain and weather conditions might appear to someone "flying around and through the landscape." These are indeed impressive and instructive, but they do not animate "change." Visualizing temporal changes in landscape ecology requires a static observation point while animating a time series as viewed from that perspective. Research is now beginning that will add the time dimension (in the form of multiple-image dates) to this capability.

What has not been attempted yet is to adapt the technology for 3-D modeling of vegetation cover—that is, to assess the structure of plant communities in the spatial domain. Data sets that would permit this kind of analysis are not available either. Unlike geologic, atmospheric, and oceanographic applications where vertical profiles are standard measurement attributes (i.e., well logs, depth soundings, balloon soundings), vertical structural profiles are not a common measurement in botanical and ecological studies. Certainly they are not acquired systematically, although one economic means for getting them would be to use low-altitude aerial mapping photography. The needs of the global species information system, and the GISs that will interface with it, will surely impact future data types and their collection strategies. But, as Ellefson & Kaiser (1990) have suggested, it is not just for the species information system or GIS modeling that such developments are emerging. They cite global change issues and improved forest planning and management as driving forces behind the need to develop new methods in forest research.

## Summary

Accurate locational and ecophysiological data for most dominant species may be relatively easy to incorporate into image-based and object-oriented databases, even today. Similar data for rare and endangered species and even dominant species at the periphery of their ranges, however, still require data collection, and this must be done by using less time-consuming and less costly means. It is not unreasonable to imagine that in our drive to collect massive amounts of environmental data and make measurements of current earth resources, we will design "new-age" botanists who are equipped with more than plant press, hand lens, ruler, and knapsack. New-age botanists will have voice, data, and video links to their home institutions, as well as to the world's major herbaria and centralized data repositories. In the future, they will be able to predict and visualize the impact of environmental changes on flora and vegetation, assess the potential impacts of varying economic development scenarios, and better manage ecosystems and communities at risk. Emerging technologies that will foster these improvements include 256 MB processing chips; seamless integration of spatial and nonspatial data sets; pedabyte storage capabilities; advanced computer networks, local area networks, and client servers; advanced visualization capabilities; advanced telecommunications systems; and miniaturization of electronic field and herbarium equipment.

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# DATA BANKING AND THE ROLE OF NATURAL HISTORY COLLECTIONS[1]

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## Abstract

A variety of strategies is being used to capture information from natural history specimens and to develop new research databases containing information on taxonomic groups. Consortia of institutions are being formed for the purpose of capturing data and making them available through centralized or dispersed databases. Geographical information, when analyzed using Geographical Information Systems, provides information useful in management and conservation of taxa and habitats. Images, when analyzed using such techniques as X-ray computed tomography and three-dimensional image processing, can reduce the need to examine actual specimens. Image, sound, and text data are being combined into research and instructional programs. Information on characteristics, distributions, and relationships of taxa are being linked to other data sources, from both collections and non-collections databases. Efforts are underway to develop data standards and data-sharing protocols in order to facilitate sharing of these data among institutions and across disciplines.


Natural history collections provide a rich information resource about our natural world. The past several years have seen administrators of systematics collections and systematists placing greater emphasis on providing improved access to collections data and supporting the synthesis of information from collections. New directions in research, a broadening of users of systematics information (from environmentalists and natural resource managers to science educators), coupled with relatively recent advances in computer technology, have been the driving forces. The result is a significant shift in purpose and expansion of collections-related databases, from the traditional databases serving primarily as indexes to the physical collections, to ones that are capable of being used as true research and educational tools.

The traditional catalog or database (for example, specimens in a herbarium) contained a relatively small core of text information about a single museum's collections. Within the botanical community, core information entities are usually contained in the specimen "label" and have included specimen identity, locality and date of collection, collector, field number, and for some organisms, substrate. When only parts of a plant are collected, some morphological features (e.g., overall size) have been noted. Additional data, such as the habitat in which the organism occurred, or other organisms with which it occurred, have often been included. Other information may also be placed on the label, e.g., chromosome counts or ethnological information, or a reference to a publication or repository. The place and method of storage for each item have also been recorded.

Unless computerized, or otherwise cross-indexed in some way, none of this information is readily available from the stored collections themselves. To find specimens from a specific locality, the entire collection must be searched manually. Similarly, to re-create an itinerary for a collector whose field book is not extant, it is necessary to comb the holdings for collections made by that collector.

These traditional catalogs or databases, if automated at all, often cover only a small portion of an institution's collection, making them minimally useful as research tools. So, although the collections were considered an extremely rich information resource, their utility was largely a potential yet to be realized. The adage, "data rich but information poor," seemed to apply.

## Current Data Banking Strategies and Projects

Today, the picture looks quite different with regard to data banking. The systematics community has undertaken multiple strategies to expand specimen-based databases and develop new research databases containing derived, rather than primary, collections data (e.g., taxon-based databases). In addition, collections data have been in-

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tegrated with non-collections data sources to provide a richer information resource. One can summarize the community's current, primary strategies in data banking efforts as follows:

1. Rapid automation strategies for specimen-based data in order to bring entire collections into an automated database.
2. Coalescing of a single discipline's specimen data from multiple institutions into a centralized, easily accessed database.
3. Employing a variety of new tools, from analytical tools to authoring (software) tools.
4. Incorporation of new data types (e.g., image and sound samples) with traditional text data.
5. Expansion of collections-related databases by including new data elements, both primary and derived, or by linking these databases with non-collections-related data sources (e.g., chemical databases).
6. Integration of collections data across disciplines.
7. Integration of system architectures across departments within an institution and across institutions.

Three current projects exemplify the first two strategies of rapid computerization of collections data and coalescing of that data into centralized databases.

The Southeastern Regional Floral Information System (SERFIS) has as its objectives: (1) to develop a centralized database composed of label data of specimens in herbaria of the southeastern United States; (2) to provide data management and storage for these data; (3) to provide technical assistance and support to these herbaria; and (4) to participate in national and international attempts to establish computerized access to specimen label data (Macrander & Haynes, 1990). Label images are captured at each herbarium, stored in digital form, then entered into the database at the University of Alabama. Each herbarium receives its data back in computerized form, and each has access to the central database via a network connection. About 100–120 herbaria are involved, covering ca. 6 million specimens, approximately 10% of the botanical specimens held in U.S. and Canadian institutions.

The Specimen Management System for California Herbaria (SMASCH) has objectives similar to those of SERFIS, but its strategy for data collection is different (Duncan, 1991). The Association of California Herbaria has devised a plan whereby its three largest members, the California Academy of Sciences, the University of California, Berkeley, and Rancho Santa Ana Botanical Garden, each have responsibility for entering data from about one-third of the largest California families. Once this phase is completed, coordinated data entry of the remaining families for each institution and for the remaining institutions will be undertaken.

About 53 institutions and 6.5 million specimens (10.8% of the total U.S. and Canadian holdings) will be involved. Data entry and access will take place over NSFNet between institutions and local area networks within institutions. Images primarily from a collection of photographic slides will begin to be scanned as part of the project.

The Inter-Institutional Database of Fish Biodiversity in the Neotropics is a major effort to build an international database bringing together information from all major collections of neotropical fishes, initiated by the Academy of Natural Sciences of Philadelphia, the University of Michigan Museum of Zoology, and Cornell University. It will make available systematic and geographic data from specimens deposited in collections in North, Central, and South America and in Europe. It includes a Geographic Information Systems interface, an electronic atlas of neotropical type localities, and remote access features. This effort uses the software MUSE for its central database. MUSE has been developed for and used by the ichthyological community at many institutions. MUSE recommends adherence to a "primary" data set and structure but is flexible in how the "secondary" data, which are less likely to be exchanged, are handled.

These three examples all provide access to collections data from more than one institution, and thus they each require integration of data across institutions.

The third and fourth strategies, employing new tools and expanding the traditional catalog with new types of data such as images and sound samples, are particularly well-exemplified by the following projects.

Geographical Information Systems (GIS) when linked with collections databases offer powerful analytical capabilities. They provide new information about the locality from which a specimen was collected, and they can be used to analyze complex relationships between the distributions of taxa, their characteristics, and their relationships with other taxa. Various current projects analyze precise locality information from systematics collections using GIS (1) to manage and conserve individual taxa and (2) to manage geographical areas and habitats. The Illinois Natural History Survey combines data on natural features, man-made features (roads,

pipelines, etc.), and distributions of individual collections, to make recommendations about planned land use in light of its impact on the environment. The survey can use the same data to determine the physical and ecological requirements of individual taxa for either research or management applications. Information on the location of organisms was used to suggest locations for the Superconducting Super Collider (SSC), a high-energy physics research facility under the auspices of the U.S. Department of Energy. The extensive database maintained by the Natural History Survey on the wildlife and plants of Illinois, including their distribution and abundance, their habitats, and their life histories and status within the state, was supplemented with computerized databases on wetlands, natural areas, soils, property boundaries, and other information necessary for siting the SSC and evaluating its potential environmental impacts (Joselyn, 1988). The Survey uses similar data to predict distributions of taxa. For example, county records for a water beetle, *Haliplus tortilipenis*, were compared with such information as average January temperature, annual precipitation, and percentage forest cover. GIS was used to determine which other counties have ecological parameters similar to those of counties within which the beetle is known to occur. That is, to determine which counties have the same combination of temperature, precipitation, and forest cover as the counties where collections of the beetle have been made. Based on this information, a hypothetical distribution range can be mapped showing areas where the species might be expected to occur.

The Illinois Natural History Survey also uses knowledge of habitats and collecting patterns to help "clean up" locality and mapping data. For example, fish can be assumed to have been collected in water, so collection sites that do not fall within a water body can be "snapped" to the nearest stream. Unfortunately, when more than one stream is nearby, the correct choice may not be made. Collections are often made at bridges or near roads, and that information can be used to influence which stream site is chosen by the computer. The best solution, according to Warren Brigham at the Survey, is to sit down with the collector in front of a terminal on which streams, bridges, and roads can be displayed and ask the collector to show where the collection was actually made.

Similar, but even more sophisticated GIS methods are used by the Environmental Resources Information Network (ERIN) in Australia to increase the accuracy of computerized collections information (Slater & Noble, 1991). Australian natural history institutions are collaborating among themselves and with the ERIN Unit, a part of the Australian National Parks and Wildlife Service, to computerize their collections following community-adopted standards and protocols. Data are transferred from the institutions into the central ERIN database and can be used in GIS and other applications. ERIN uses a climatic file, called BioClim, that incorporates data from thousands of data-gathering locations for 16 climatic parameters such as wet season rainfall maximum, wet season rainfall minimum, and wet season maximum temperature. By mapping reported localities for a taxon, a statistical analysis can be used to identify specimens that fall outside the typical climatic range for the taxon in any one or a combination of parameters. Those specimens can then be checked to see that they have been correctly identified and that the locality was recorded correctly. BioClim data can be used as a modeling tool by adjusting any one of the 16 parameters, which results in associated dependent changes in the rest of the parameters. The current climatic requirements of species can be inferred from the species' current distributions; thus, if the distribution of a given climatic type is changed the concomitant change in species distribution can be predicted. This information can be used to determine whether natural area preserves are available in the predicted future climatic zones to provide refuge for sensitive taxa.

A new tool of the medical profession, and one that a number of researchers at the Washington University School of Medicine (St. Louis) have employed and studied, is X-ray computed tomography combined with three-dimensional image processing (Hildebolt et al., 1990). This technology enables scientists to conduct research without physically damaging specimens. It also improves the ability to make new measurements and preserves images of objects that must be returned to their places of origins. Physical anthropologists at the National Museum of Natural History (Smithsonian Institution) recently completed a prototype in which two-dimensional image slices were produced, then used to produce three-dimensional reconstructions that show both the exterior and interior surfaces of specimens and objects. In the future, one may find these types of images commonly associated with museum collection databases and available by network to other researchers.

The relatively new authoring tools that enable creation of interactive monographs and tutorials have been used in several recent projects aimed at science education and the identification of specimens. As part of the Biological Curriculum In-

novation Study (BioCIS) led by Chad McDaniel of the University of Maryland, Smithsonian Institution researchers have been working on the development of introductory college-level biology courses through the production of hypertext multimedia databases that document aspects of biological diversity. These applications combine text, image, and sound from a variety of museum information sources. Projects being undertaken include a database of information on mammal species of the world, an application documenting collection and processing of botanical specimens, an identification manual for crocodiles and their products, and an application that allows the user to "deforest" the Amazonian rainforest while learning what species can or cannot live in the remaining forest fragments.

A botanical project similar to BioCIS has been envisioned by Arturo Gómez-Pompa of the University of California, Riverside. His prototype, Q-Taxa, incorporates images of specimens, living plants, drawings, maps, plus specimen information and taxonomic information in an environment that invites exploration by both layman and researcher (Gómez-Pompa & Plummer, 1990).

Programs for producing descriptions and interactive keys from sets of characters and character states, DELTA, have been written by Michael Dallwitz and Les Watson of CSIRO (Australia). An interactive key to cultivated plants in North America using hypertext is being developed by Larry Ragan at Pennsylvania State University. Interactive keys to families or to taxa within individual families are also available, e.g., a family key from T. Duncan, a key to Australian rainforest trees by B. Hyland, and a key to the orchids of Great Britain by R. Pankhurst. Although such files are not derived directly from specimen data, they are a product of the expert staff associated with natural history collections and are important tools in curation and education.

The fifth strategy supports information synthesis in two ways: (1) by broadening collections-related databases beyond the traditional specimen "label" database to include both primary and derived data, and (2) by linking collections-related databases with other, non-collections-derived sources.

The first of these two ways is exemplified by the Hymenoptera Database System (HDS) and Flora of North America (FNA). They are taxon-based online databases. HDS is maintained by systematists at the U.S. Department of Agriculture and National Museum of Natural History, and FNA is maintained by the Flora of North America project at the Missouri Botanical Garden.

The Hymenoptera Database System contains systematic and biological information on about 18,000 species of saw flies, parasitic wasps, true wasps, ants, and bees (see Krombein et al., 1974, for a description of earlier phases of this project). The project has integrated data from both entomological and botanical sources, one botanical source being Index Nominum Genericorum, a database of all validly published generic names for plants (Farr et al., 1979, 1986). The HDS contains literature references on taxonomy, biology, and morphology for described taxa. Information is provided on geographic range, ecology, whether introduced or adventive (accidently introduced), plant or animal hosts, parasites, predators and prey, pollen preferences, and flowers visited. A wide variety of queries can be made from this database, e.g., a biological control specialist could ascertain the names of parasitic Hymenoptera introduced from other parts of the world and successfully established in the United States, and obtain information on their known distributions.

Flora of North America is a binational, multiinstitutional project to produce a floristic treatment of the vascular plants and bryophytes growing outside of cultivation north of Mexico. In addition to 14 published volumes, the project will produce a taxonomic database containing information on the relationships, characteristics, and distributions of the plants. A key feature of the FNA project, as with most floristic and faunistic projects, is that it provides authoritative data on the plants. Flora of North America, while accumulating morphological data in a traditional manner, captures that morphological data in a database (TROPICOS, developed at the Missouri Botanical Garden) that allows analysis of correlations among taxa, and among characteristics. Moreover, Flora of North America, by integrating morphological data with collections-based, mappable distribution data, can provide a tool for studying the relationship between morphological characteristics and the physical parameters within which the plants occur (Morin, 1991).

Furthermore, taxonomic databases like HDS and FNA can serve as connecting points to link disparate data using a taxonomic framework. An independent query might ask for the chemicals produced by plants that occur on a certain soil type. Specimen information mapped using GIS against soils gives the names of plants that occur on the soil type in question, and those names can be used in turn to query a remote phytochemical database to get a list of the chemicals they are reported to produce. The number of databases that can be linked through the taxonomic framework is unlim-

ited but includes ethnological, reproductive, anatomical, genetic, specimen-based, and bibliographic data.

Researchers in the Evolution of Terrestrial Ecosystems Program (ETE) (University of California, Santa Barbara, and National Museum of Natural History) have initiated the ETE database to allow broad-scale comparisons of the paleobiology and paleoecology of terrestrial ecosystems, plus their plant and animal communities. The ETE database will document and compare plant and animal assemblages from the Silurian to Recent times and will establish patterns of similarity and novelty in terrestrial ecosystems. Researchers can then determine the degree to which ecological roles of organisms and structural characteristics of ecosystems have changed. These patterns will then be the basis for assessing the impact of environmental conditions on ecosystem structure, and the relationship of such phenomena to evolution within specific groups of organisms.

The ETE database incorporates both primary and derived information about fossil localities and the plant and animal species collected from them (Damuth, 1991). For each locality, in addition to its name, age, and location, there are fields for sedimentological, taphonomic, and paleoecological data. Each locality has a species list (vertebrate, plant, or invertebrate). For each species there is a taxonomic classification and a set of morphological and ecological descriptors that vary with the type of species. A locality-species table associates localities and species and records relative abundance of species at a given locality. The bibliographic table contains publications that were sources of information for the database. The museums table records which museums have material and from which localities. The time units table names geochronological units and their associated maximum and minimum ages (in years). Last, the sedimentary structure and taphonomic table records observations relevant to depositional environment.

An example of linking collections-related data to other data sources is the Environmental Protection Agency–National Oceanographic Data Center (EPA-NODC) Taxonomy System modernization effort. The EPA recently turned to systematists at the National Museum of Natural History, U.S. Department of Agriculture, National Marine Fisheries Service, and the U.S. Fish and Wildlife Service to help improve an existing taxonomic system by developing an underlying logical data model for taxonomy. The database includes valid scientific names, synonyms, and common names. Each valid scientific name is associated with a single taxon of a higher rank, and each synonym is associated with a valid name. The database provides all taxa contained within a higher taxon, scientific names corresponding to common names, and common names applied to any scientific name. The system is seen as critical to supporting EPA's Environmental Monitoring and Assessment Program and Office of Water Quality. The database enables field biologists to associate data recorded in the field or laboratory (water chemistry, locations, numbers of organisms, and biomass) with a taxon. Interactive access between the taxonomy system, the Ocean Data Evaluation System, and a biological survey system called BIOS are planned.

The last two strategies are essential to laying the groundwork for broader-scale information synthesis. These projects may well support the next major step in providing access to natural history collections. These efforts involve standardization of "data architectures" (e.g., definition of data parameters) and development of protocols to allow data sharing across systems. The International Working Group on Taxonomic Databases in the Plant Sciences (TDWG) is an organization that has attempted to establish standards, if none exist, for various data elements in plant taxonomic work, expressly for the purpose of facilitating data exchange, and it is one of several organizations that have efforts underway in these areas. The Association of Systematics Collections Computerization and Networking Committee has also initiated an important effort to develop these standards across all systematics collections.

A systems architecture undertaking is being led by a group from the largest free-standing (non-university associated) natural history institutions and botanical gardens in the United States. The member institutions have agreed to participate as a consortium to plan modernizations of their collection and research information management environments. The purpose is to install at each institution new equipment and software to support research needs, enhance collections management, and improve interconnectivity within and among the consortium institutions. An example of a similar undertaking within a major institution is the new project at the University of California, Berkeley, to integrate data from the various museum collections throughout its campus. This would allow, for example, linking archeological, ethnobotanical, and taxonomic information together on an institutional network. Other institutions are planning to connect integrated online library systems to their research databases to allow direct linkages of library information to research-derived data and vice versa.

## Conclusion

These new approaches all support a primary goal of the nation's systematics collections institutions: to improve information availability to our systematics researchers and to a growing community of information users, including environmentalists, conservationists, and science educators. To achieve this goal, new working relationships have been formed within and among organizations, across taxonomic disciplines, and between systematists and information science and engineering professionals. The new technology makes available entirely new categories of information that now can be derived from collections, and it provides new tools with which to analyze and use both traditional and new kinds of information for research and resource management.

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# THE NATIONAL SCIENCE FOUNDATION: FINANCIAL, INTELLECTUAL, AND KNOWLEDGE BROKER FOR SYSTEMATIC BIOLOGY[1]

*James R. Estes*[2]

ABSTRACT

The National Science Foundation (NSF) is the primary financial broker for systematic biology, with NSF funding most basic systematic research in the United States. Systematists generate ideas in the form of proposals to the Foundation, which are subject to merit review by peers. This review process has the potential to enhance the science and, therefore, constitutes one facet of intellectual brokering. Program officers, in turn, react to the proposals and their reviews in making recommendations for awards, and in the process interact with the Principal Investigators (PIs) to provide intellectual counsel. NSF also plays a proactive role in the intellectual brokering of systematics through (1) sponsorship of study groups, workshops, symposia, and conferences; (2) development of initiatives; (3) funding of Small Grants for Exploratory Research (SGER) proposals; and (4) funding Special Creativity Extensions (SCE) to existing NSF awards. Whether reactive or proactive, NSF generally functions early in the research enterprise; the Foundation is not a direct player in knowledge synthesis and analysis—the Foundation does not disseminate the data and results from the projects it funds. Rather, it relies on the scientific community and its system of peer-reviewed journals and indices. However, NSF does fund innovative proposals to develop databases; to computerize museum collection-label data; and to exchange specimens, data, ideas, and syntheses. In this way, NSF does contribute to knowledge and/or data transfer. Information and ideas gained from NSF-supported research efforts could be diffused directly into society-at-large by coupling proposals for scientific studies with proposals for formal and/or informal educational programs. Systematic biologists are in an ideal position to take advantage of any such funding opportunities because of the already extensive interactions that occur between natural history museums and members of the systematic community.

President Harry S. Truman signed the National Science Foundation Act of 1950 (Public Law 81-507) to culminate a decade of debate about the structure and function of the agency. This law with its various amendments provides the National Science Foundation (NSF) authority to promote research in the United States, and in that role, NSF has been a benefactor of basic scientific research (England, 1982). This is especially true for systematic biology, because NSF provides more than 90% of the federal funding awarded to U.S. colleges and universities for studies of phylogeny, classification, and biodiversity (BBS Task Force, 1991).

## NSF AS FINANCIAL BROKER FOR SYSTEMATIC BIOLOGY

During the half-century of NSF's existence, new comparative techniques and methods of analysis have emerged to transform systematic biology, in general, and plant systematics, in particular. The most compelling element in this transformation has been the coupling of molecular and computational biology. The field of plant systematics has also been aided and abetted by the conservative nature of the chloroplast genome. The emergent field of plant molecular phylogenetics has developed so rapidly that a rigorously determined and testable phylogenetic framework for the green plants is already well within our reach (Palmer et al., 1988). Phylogenetic relationships within large and complex families, such as Asteraceae, Fabaceae, and Poaceae, are also yielding to molecular analysis with high levels of resolution (Jansen et al., 1991; Lavin & Doyle, 1991; Lavin et al., 1990; Soreng et al., 1990). It is even possible to probe evolutionary divergence deep within the hierarchy of life using data from molecular sequence analyses of extant taxa and microfossils from deep strata, embedded

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as always within the modern evolutionary paradigm (a small sampling of papers includes Buchheim et al., 1990; Gajadhar et al., 1991; Knoll, 1992; Lake, 1991; Palmer et al., 1988; Schlegel, 1991; Woese, 1987). The resulting phylogenetic inferences can then be used to interpret patterns and derive syntheses in fields as diverse as biogeography, behavior, and development (Brooks & McLennan, 1991). These advances would have scarcely seemed possible even a decade ago.

Systematists have also sounded a clear signal that the world faces a crisis over the loss of biological diversity (National Science Board, 1989; Prance, 1984; Solbrig, 1991). This realization has resulted in a renewed interest in surveying and cataloging the world's biota and the consequent writing of floras and faunas (Heywood, 1984b). In this effort, systematists are also beginning to employ more sophisticated systems for data storage and retrieval to ensure that the locality data for each specimen and the descriptions and nomenclature for each taxon can be readily retrieved; thus the flora or fauna can be efficiently and effectively revised (Bisby, 1984; Dallwitz, 1984; Gibbs Russell, 1989; Pankhurst, 1974). Watson et al. (1986) have effectively used this approach for the grasses of Canada, and a consortium of African botanists are accomplishing the same for the entire *Flora of Southern Africa* (Gibbs Russell, 1989, 1990). It is possible that floristic work is at an all-time high, with several major surveys of plant diversity in the temperate and tropical zones either recently completed or well under way (Heywood, 1984a). The printed products of the most modern of these endeavors may be reminiscent of floras and faunas of the past two centuries, but they differ in having a foundation based on detailed databases, and the most forward-looking floristic projects also include equipment for the highly precise determination of map coordinates and involve the potential for interacting with Geographic Information Systems (Rodman, 1989).

This is surely one of the most exciting periods in the history of systematic biology, in part because so much seems within our grasp, but also because we realize the magnitude and importance of the tasks before us.

It is arguable that these, and other, major developments would have transpired in the absence of NSF. However, it is undeniable that the Systematic Biology Program (Table 1) provided funding for much of the development of the theory and techniques of systematic biology: the collection of specimens and data and the interpretation of results that has fueled this burgeoning of systematic biology. In addition, officers of the Systematic Biology Program established a special competition for survey and inventory research (NSF, 1990d), by allocating approximately $2.3 million exclusively to fund floras and faunas. This competition now forms the basis of the newly erected Biotic Surveys and Inventories (BS&I), which with Systematic Biology is in the Division of Environmental Biology (DEB) (Table 1), attesting to the Division's commitment to the importance of cataloging the plants, animals, fungi, and microbes of the world. Research Collections in Systematics & Ecology (RCS&E), also in DEB, provides funds for the maintenance and computerization of those research collections (NSF, 1985a).

It is difficult to envision this flowering of the two cardinal dimensions of plant systematics—phylogenetics and floristics—without the monetary support of NSF (Table 2). With the excitement generated by these two approaches and their use in other contexts, the number of proposals received in Systematic Biology appears to be on the rise (Table 3). Additionally, both molecular and diversity studies are costly—the former requires a large budget for supplies and materials and the latter for travel and fieldwork; both are labor intensive. As a consequence, this past year also saw a dramatic increase in the level of requested funding (Table 3). This placed tremendous stress on a budget that has grown by much smaller increments (Table 2). Regardless, the importance of the roles of Systematic & Population Biology (S&PB) and Biotic Surveys & Inventories (BS&I) as financial brokers of systematic biology is clear and secure.

## NSF as Intellectual Broker for Systematic Biology

### Proposal preparation and review as elements of intellectual brokering

In general, funding of awards by NSF is made in response to proposals submitted by Principal Investigators (PIs), who are members of the research community. Typically this funding is based on the recommendations of program officers (POs), who are at the base of NSF's administrative hierarchy. Funding is, therefore, a grass-roots phenomenon both in the community and at NSF, and the decisions concerning funding or declination of proposals at NSF is primarily reactive. That is, POs in S&PB and BS&I respond to proposals that result from the pool of systematic biologists. Thus, as noted above, POs are important players in the financial brokering of the science, but decisions concerning funding are also at the intersection of

TABLE 1. Reorganization of the programs in environmental biology at NSF. The core of the Systematic Biology Program (represented in greater detail than the remaining programs) was recently united with elements of Population Biology to form the Systematic & Population Biology Cluster (also represented in greater detail than the other clusters). Systematic Biology and Population Biology continue to function as independent units for budgetary and proposal review purposes; although, some programs such as Molecular Evolution may have special panels that are managed by program officers from any of several divisions and programs. The Ecology and Ecosystems programs have also merged to form the Ecology Studies Cluster. A third cluster, Long-Term Projects in Environmental Biology, was formed from the Biological Research Resources Program and the long-term projects unit from Ecosystems. PIs should contact programs officers concerning the submission of proposals in particular research specialties. Only applicable programs are shown in the Division of Integrative Biology and Neurosciences.

| Previous organization | Present organization |
|---|---|
| Directorate for Biological, Behavioral & Social Sciences (BBS) | Directorate for Biological Sciences (BIO) |
| Division of Biotic Systems & Resources (BSR) | Division of Environmental Biology (DEB) |
| Ecology Program | Ecological Studies Cluster |
| Behavioral ecology | Community Ecology Program |
| Community ecology | Ecosystems Program |
| Population ecology | Integrative & Theoretical Ecology Program |
| Ecosystems Studies Program | Population Interactions Program |
| Integrative ecology | Systematic & Population Biology Cluster |
| Systems ecology | Morphological & Molecular Phylogenetics Program |
| Population Biology & Physiological Ecology Program | Taxonomy & Classification Program |
| Behavioral, morphological & molecular adaptation | Classification theory |
| Life-history studies | Revisions |
| Molecular evolution | Biogeography, Coevolution & Paleobiology Program Speciation |
| Physiological ecology | Molecular Population Biology |
| Population genetics | Population & Quantitative Genetics Program |
| Systematic Biology Program | Life Histories & Population Dynamics |
| Biogeography | Long-Term Projects in Environmental Biology Cluster |
| Classification theory | Research Collections in Systematics & Ecology Program |
| Functional morphology | Biotic Surveys & Inventories Program |
| Phylogenetic analysis | Division of Integrative Biology & Neurosciences (IBN) |
| Speciation | Physiological & Functional Ecology Program |
| Surveys and inventories | Animal Behavior Program |
| Taxonomic revisions | |
| Biological Research Resources Program | |
| Collection support | |
| Monograph support | |

financial and intellectual brokering. This results because the continuing dialog between the PO and PI has substantial room for discussions of the science itself. These discussions range through time from initial deliberations concerning an idea for a research project through discussions of the reviews of the proposal.

At the critical first step in the process, scientists interested in submitting a proposal may contact the relevant PO, with telephone or electronic mail being the most effective means of communication at this time. POs can often provide counsel regarding the potential viability of a project in the process of merit review. Frequently, suggestions can be offered that might direct the PI to a focus or protocol that has the potential to improve materially the research proposal, and more importantly, the proposed research. The following hypothetical cases provide examples of the advice POs might offer prospective PIs: (1) an indication that a proposed flora has a lessened chance of being recommended for funding by the Biotic Survey and Inventory Advisory Panel unless a meaningful and useful database is included; (2) a comment that reviewers react more favorably to proposals in molecular systematics if the inferred phylogeny is then used to comprehend other radiation patterns in the taxon; and (3) a suggestion that a monograph with a rigorous analysis of the phylogeny of the taxa would be a more meaningful contribution than *only* a set of keys and descriptions. Of course, the advice carries no guarantees, and the PIs are free to accept, decline, or modify the suggestions, but whether or not these proposals

TABLE 2. Funding history in Systematic Biology Program, fiscal year 1985 to fiscal year 1992, in millions of dollars. All figures are from NSF Budget Requests to Congress except for bracketed figures, which indicate Current Plan or Estimates. FY'86 budgets were reduced by Gramm-Rudmann-Hollings sequestrations. BIO—Directorate for Biological Sciences; DEB—Division of Environmental Biology; SB—Systematic Biology Program.

| Fiscal year | NSF | BIO | DEB | SB |
|---|---|---|---|---|
| 1985 | 1,500 | 245 | 58 | 12.2 |
| 1986 | 1,523 | 262 > 239 | 61 > 58 | 12.2 |
| 1987 | 1,628 | 259 | 58 | 12.7 |
| 1988 | 1,718 | 266 | 59 | 12.4 |
| 1989 | 1,886 | 281 | 63 | 12.7 |
| 1990 | 2,026 | 294 | 67 | 13.7 |
| 1991 | [2,316] | [315] | [71] | [14.4] |
| 1992 | [2,722] | [356] | [78] | [15.9] |

TABLE 3. Number of proposals submitted and total funding requested in Systematic Biology Program, fiscal year 1985 to fiscal year 1991. Requests in millions of dollars.

| Fiscal year | Number of proposals | Funds requested |
|---|---|---|
| 1985 | 348 | $52.4 |
| 1986 | 330 | $50.5 |
| 1987 | 348 | $55.1 |
| 1988 | 335 | $54.0 |
| 1989 | 326 | $60.0 |
| 1990 | 347 | $64.8 |
| 1991 | 361 | $79.2 |

are funded, the modified research will likely be more significant and have a broader impact on systematics if the recommendations are given careful consideration.

The Foundation is deeply rooted in the academic tradition of merit review. Accordingly, most programs in DEB employ the advice of practicing scientists by (1) mail-solicitation of reviews from specialists in some aspect of the proposed research and (2) convening advisory panels composed of scientists with broad expertise prior to making their own recommendations for awards. This practice provides for a much more thorough review. Perhaps just as importantly, a thorough and critical review elicits suggestions that sharpen the focus, clarify the goals, and improve the protocol of the proposed research. In brief, the review system should have a salutary scientific impact on each proposed project and the PI, and ultimately then on the entire field. Peer review, including review by the POs, is the most important element in the intellectual brokerage practiced by NSF because it can most directly influence individual PIs, albeit the reviews are available only to the individual PI, and then only after the proposal has been funded or declined. The "Panel Summary" is the most important document in this phase of intellectual brokering because it fixes the proposal under consideration within the context of modern systematic biology, and because it identifies both the flaws and strengths of the proposed research. The individual reviews, however, generally are more detailed and cover specific issues concerning taxon and character selection, methods of data collection and analysis, and the potential systematic and taxonomic impact of the work. There is, therefore, considerable responsibility thrust upon a scientist selected to review a proposal, and that responsibility is partitioned between the responsibility of being fair to the PI and being rigorous for the science. Regardless, reviewers should always attempt to improve the proposed work and hence the science.

For this aspect of the system of intellectual brokering to function effectively, it is essential that reviewers write substantive, even if succinct, reviews in which they provide a detailed analysis of both the strengths and the weaknesses of the proposed scientific problem and the research protocol. In some instances, reviewers may have knowledge of only one or a few aspects of the proposal; however, it is incumbent on these reviewers to criticize that aspect of the proposal in which they are expert. Only then does the PI receive the intellectual assistance necessary for development and the Panel and the Program obtain sufficient data to make an informed recommendation. The routine assignment of unqualified ratings of "excellent" or "very good" for all proposals to study particular taxa or to investigate certain processes seldom, if ever, helps the PIs during the Panel's discussion of proposals, and it deprives PIs of the reviewer's expertise. If a proposal is truly excellent, it is vital that the reviewers explicitly and precisely explain in what ways it excels, because panels and programs almost exclusively use the narrative, rather than the rating scale, of the Proposal Evaluation form.

Funds allocated to the programs in systematics, that is S&PB and BS&I, probably always will be insufficient to fund all of the proposed systematic research that is worthy of accomplishment. (It is arguable that such levels of funding would actually have a dampening effect on innovation and advances such as those described for plant molecular phylogenetics.) Rather, because of its limited bud-

get, the Systematic Biology Program must, and should, focus on research that will advance the field, that is thorough and in depth, and that will have an impact beyond the boundaries of the taxon under investigation. It is precisely in this funding environment that reviewers, panels, and program officers can be most creative influences in the discipline. For instance, it seems obvious that POs in the Systematic Biology Program over the period from 1980 to 1989 responded to and encouraged the development of molecular systematics while maintaining the legitimacy of the review process. This creative management of the program was instrumental in the rapid development of molecular systematics and molecular evolution (Goodman, 1992; Goodman et al., 1992) and made possible the breakthrough in understanding phylogeny and evolution of the Plant Kingdom. All the while the Program continued to fund meritorious proposals that were based on other comparative techniques, both traditional and new (Committee of Visitors for the Systematic Biology Program, 1991). At the end of the last decade, the Program also made a bold decision to establish the Survey and Inventory competition, thus enhancing our knowledge of the world's biodiversity.[3] As the new decade opens, the Program will undoubtedly identify other promising new vistas, perhaps including new approaches in systematic biology to understand phenotypic evolution, biogeography, and ecology based on and in the context of phylogenetics (Brooks & McLennan, 1991); the development of algorithms that permit phylogenetic analysis of hybrid complexes; and the refinement of methods of estimating phylogeny using developmental pathways. All the while, the Program must continue to fund the most innovative molecularly and morphologically based phylogenetic analyses and taxonomic revisions. Nevertheless, this phase of intellectual brokering can only be reactive, and somewhat conservative. Other avenues do exist, however, that offer a more active role for NSF program officers.

## NEW DIRECTIONS IN SYSTEMATIC RESEARCH

In addition to funding research by reacting to proposals, the Foundation is directed to initiate basic scientific research (Public Law 81-507); therefore, NSF has the authority to function as an intellectual broker beyond what is possible in the standard competitive grant programs. Appropriately, procedures exist that permit a more proactive role for program officers. This permits flexibility and the capacity to respond to new findings and techniques. Fortunately, NSF is governed and administered by working scientists. The National Science Board (Public Law 81-507) governs and sets policy for the Foundation, and many of its members are active scientists. In addition, many of the administrators in the directorates, divisions, and disciplinary programs are Visiting Scientists (often termed "rotators"), who return to research programs after one or two years in Washington. For instance, currently (i.e., June 1992) in the Division of Environmental Biology (DEB) 75% of the program officers are rotators. In addition, all of the permanent officers are research biologists, and all have taken advantage of NSF's sabbatical program by taking a year's leave in a university setting. The result is that the programs concerned with the biology of species, populations, communities, and ecosystems are steered by peers who are keenly interested in the development of their own sciences and capable of discerning trends within the disciplines.

Program officers may stimulate the launching of new fields of systematic inquiry or the re-charting of traditional areas in at least four ways, and examples will be drawn from the field of biodiversity (similar scenarios could have been described for cladistics, morphometrics, molecular systematics, or molecular evolution):

*1. Funding of study groups, workshops, conferences, and symposia.* This avenue typically involves a dialog between a PO and individual scientists, who may be the representative(s) of scientific societies. These venues provide opportunities for planning research agendas, transferring technologies, discussing common research topics, and presenting research results for a common field of study, respectively. Two examples are the following. (1) Systematics Agenda 2000 had its origins in a study group organized by the Smithsonian Institution and the Association for Systematics Collections to seek a way for the systematics community to express its views and to take action concerning the decline in global biodiversity. A broader charter evolved, and officials at NSF indicated that they would be willing to entertain a proposal to fund additional workshops and conferences. The proposal received favorable reviews and was funded. (2) The workshop on the development of a protocol for botanical surveys held in 1989 resulted from an extensive set of discussions between POs in Systematic Bi-

[3] This decision is worthy of recognition. The program officers in Systematic Biology who responded so positively and effectively are James E. Rodman, David Schindel, and William Moore. John Brooks and James L. Edwards were Division Director and Deputy Division Director, respectively, and provided support for the decision.

ology and the editors of *Flora of North America*. One result was publication of a guide for the development, management, and conduct of floristic projects, *Floristics for the 21st Century* (Morin et al., 1989), which provides counsel to PIs who intend to submit biotic survey (plant, as well as animal and microbial) proposals to BS&I. Adherence to the elements of this publication should lead to more mature and better developed proposals to conduct floristic—and faunistic—research and, not coincidentally, more innovative and useful surveys.

*2. Development of initiatives.* Initiatives provide a mechanism for obtaining additional, or new, funds for the Foundation, divisions, and programs, as well as in the federal budget as a whole. The idea for an initiative may originate at any level in the agency, but often occurs at the program officer level. Initiatives may also grow out of interactions with the scientific community, as products of workshops, recognition of proposal trends, awareness of major unresolved scientific questions, congressional action, directives from the Director of NSF, the National Science Board, or all of these.

Once again using the development of the current NSF programs in biotic surveys and inventories as an example: The directorate-wide (Directorate for Biological Sciences—BIO) competition in Basic Research in Conservation and Restoration Biology (NSF, 1990a) resulted from all of the above mechanisms, as did the Biotic Survey and Inventory competition, which arose from the reallocation of internal funds in the Systematic Biology Program (cf. National Science Board, 1989). This last-mentioned competition is now the basis for a new program (NSF, 1990d; Yates & Estes, 1992). These funds have since been augmented by funds from the U.S. Agency for International Development (A.I.D.) to support biodiversity research in developing countries and by A.I.D. and the National Institutes for Health (NIH) for a program in drug development, biodiversity, and economic development in developing countries (NIH et al., 1992; Schweitzer et al., 1991). The second of these augmentations was developed with the assistance of a workshop jointly funded by NSF. These agencies and others—such as Department of State, Department of Defense, Department of Agriculture, Department of Energy, and Department of Interior—have responded to to a widespread recognition of the need for more biodiversity research. This combined effort therefore had a compounding effect.

*3. Small Grants for Exploratory Research (SGER).* This instrument for funding is designed for investigations that are urgent or risky or that have the potential to result in new directions in basic research (NSF, 1989). They may be initiated by an investigator or, rarely, through the PO contacting a worker with appropriate expertise. Because they do not require an external review, there is a relatively rapid turn-around in funding.

Appropriately, relatively few are granted each year (five in Systematic Biology in fiscal year 1991). Of these, one provided funding to develop techniques for the study of biodiversity of free-living soil nematodes. As the Science Board (NSB, 1989) report recommended, diversity in the rhizosphere needs special attention.

*4. Special Creativity Extensions (SCE).* Programs have the capacity to grant up to two-year extensions for awards when creativity and productivity have been extraordinarily high. SCEs are made without any action on the part of the PIs; in fact, PIs cannot institute a request for such an extension. Not surprisingly, these extensions have been made sparingly.

Four SCEs were made by the Systematic Biology Program over the past three years, and one was awarded to continue a highly creative faunistic survey.

Intellectual brokering at NSF, therefore, has tended to function early in the research enterprise—it functions through initiatives and proposals. In this light, it is not surprising that the NSF direct-access database provides entry to the abstracts (equivalent to the Program Summaries that are submitted with proposals) of funded proposals. This new service, *(STIS) The Science and Technology Information Service* (NSF, 1991b), permits anyone with a modem to scan these abstracts using keyword or topical searches. Thus, it is relatively easy to ascertain if the Foundation has funded research in a particular area and to discern research trends. Other information is also accessible through the use of STIS, including the text of most NSF publications. The Systematic Biology Program also publishes an annual *Awards List* (available by writing the Program), which provides an indication of funding trends, and constitutes the Program's primary effort in direct knowledge brokering.

## NSF as Knowledge Broker for Systematic Biology

Perhaps surprisingly, NSF does not a play a significant role in the formal release or indexing of data that results from funded research projects. There are traditional and historic, as well as economic, reasons for this seeming paradox.

NSF came into being after the basic structure of the U.S. scientific enterprise was well established. Although the basic research enterprise in 1950 was, and remains, centered on colleges and universities and other similar non-profit institutions, in a real sense it consisted of a diffuse, but well-organized, suite of scientific societies with members scattered at institutions throughout the country. One service of these societies has been the dissemination of scientific knowledge among their members and the scientific community at large; as a consequence, most of the societies publish peer-reviewed journals. Most scientific societies also hold or sponsor annual meetings that encompass both independent research reports and symposia. Symposia provide fora for defining new research directions as well as summarizing important research findings. In addition, indexing services were also available in 1950; their computerized descendants provide easy, if sometimes expensive, accessibility to the literature.

The Foundation apparently accepted and placed its trust in the ability of these scientific communities to recognize and to publish the results of worthy scientific research, rather than imposing another layer of bureaucracy and reports. (This philosophy continues to be reflected in the criteria for funding of systematic monographs within Research Collections in Systematics and Ecology (RCS&E) (previously Biological Research Resources Program or BRR) (NSF, 1985b).) The decision to require relatively few and brief reports and to trust in the scientific integrity of the publication system of the societies freed PIs to concentrate on accomplishment of the proposed research, rather than on the writing of extensive, detailed reports. Because the editors, editorial boards, and reviewers work for scientific journals without real compensation, the task is accomplished efficiently, with integrity, and less expensively than if the government managed the system. Thus, NSF depends upon non-governmental agencies to monitor publication of the results of its awards. (Albeit, early in its history, NSF provided a strong foundation for continued funding of *Biological Abstracts* (England, 1982).) In my view this system works effectively and efficiently.

It would be quite erroneous to believe from this lack of direct involvement, that NSF is disinterested or that it fails to provide funding for the important task of knowledge brokering. The Foundation fosters and promotes publication of research results. For instance, publication costs are routinely included in proposal and award budgets, with the NSF budget form even including a specific line item "Publication Costs/Documentation/Dissemination" on the NSF *Summary Proposal Budget* (NSF Form 1030). NSF can also support publication of meritorious research beyond this basic level of support through competition for monograph publication costs within RCS&E as mentioned above. Pertinent for plant systematics, this program subvented the publication of *Systematic Botany Monographs* through its foundling stages, promoting the spectacular success the journal has enjoyed.

NSF requires listings of publications and reprints for the PI's final project report—required of all funded projects—and it requires the inclusion of the section "Results from Prior NSF Support" (NSF, 1990c) for all grant applications where the PI or co-PI has received NSF support in the previous four years. Clearly both these exercises are for the convenience of the review system and are not intended as mechanisms for the dissemination of research syntheses.

The development and maintenance of electronic databases should follow pathways similar to those for the review and publication of research journals. That is, the society or community that collects and uses the data should provide the organizing elements and expertise for the database. NSF already provides seed funds for those database projects that are considered meritorious (NSF, 1990b). The Human Genome database is a prime example (Cinkosky et al., 1991; Roberts, 1991; Salton, 1991). Other databasing needs that involve the systematic community include ongoing attempts to make the data in museums and herbaria more accessible and useful (Bisby, 1984; Gibbs Russell, 1989; NSF, 1990b; Stuessy & Thomson, 1981). RCS&E currently provides funding for collection management, specimen databases, and electronic networking in museums and herbaria (NSF, 1985a). There may also be a need for a central facility for plant molecular sequences and their alignment for the development of phylogenies and another for electronically stored phenotypic data for automated description and key software. It is unclear what the impact of the *Global Change Research Act of 1990* (NSF, 1991a; Public Law 101-606) will have with respect to databases, but clearly it calls for data collection and management of information that is highly relevant to systematic biology, and there will be clear opportunities for the discipline and the research collections.

Perhaps NSF's most influential role in the synthesis of research results is through the funding of symposia, either those in association with the annual meetings of societies or symposia that are free-standing. Once again, NSF is dependent upon

TABLE 4. Funding by Country for Biodiversity in Developing Countries Joint NSF/A.I.D. Competition, fiscal years 1990 and 1991. Total awards = $7,166,220 (NSF funding = $4,677,220; A.I.D. funding = $2,489,000).

| Country | Number of awards | Country | Number of awards |
|---|---|---|---|
| Argentina | 1 | Madagascar | 2 |
| Bolivia | 2 | Malaysia | 1 |
| Brazil | 8 | Mexico | 2 |
| Chile | 2 | Namibia | 1 |
| Colombia | 1 | Nicaragua | 1 |
| Costa Rica | 7 | Panama | 1 |
| Dominican Republic | 1 | Philippines | 2 |
| Ecuador | 1 | Thailand | 1 |
| Gabon | 1 | Venezuela | 1 |
| Indonesia | 1 | Total | 37 |

the research community to recognize the need for syntheses and to write creative proposals for funding. The Annual Systematics Symposium at Missouri Botanical Garden provides one example of NSF funding for meetings that focus entire fields of research, such as the methods of phylogenetic analysis within the Plant Kingdom, the subject of the 1992 symposium. The previously cited *Floristics for the 21st Century* (Morin et al., 1989) accomplished the same goal for floristic research. One final example is the recognition by the ecological community of the need for a center for ecological synthesis and analysis. Accordingly, a proposal was submitted to the Foundation by James H. Brown and Stephen R. Carpenter on behalf of that community for a workshop to complete a needs assessment and task analysis for the establishment of such a national center. Although program officers can stimulate such applications, it seems clear that the ideas are most likely to emerge from the scientists themselves.

## Opportunities for Expanding the Impact of Systematics

I believe that Systematic Biology is a viable scientific discipline with profound implications for humankind. That viewpoint is not, however, universally understood, or perhaps even accepted. There are two great arenas where systematists need to act with vigor to change that perception: (1) developing countries and (2) the American public. Members of our community are already actively engaged in the former domain, although there is much yet to be done. The latter arena promises a more truculent foe, ignorance. There may be a general lack of public understanding of such basic issues as cause and effect, adaptation, evolution, food webs, the role of natural systems in sustaining human populations, humans as organisms, et cetera, et cetera.

TABLE 5. Criteria for funding in the joint NSF/A.I.D. program Biodiversity in Developing Countries.

1. Scientific merit.
2. Impact on host country and its biological diversity:
   a. Conservation of biological diversity.
   b. Contribution to sustainable use of biotic resources.
   c. Significance to development of biodiversity infrastructure.
   d. Effect on economy or on the economic role of studied species or habitat on the economy.

## International Development and Systematic Biology

The community of U.S. systematists, working in concert with NSF and the U.S. Agency for International Development, has had a long and important presence in the Neotropics. These government agencies and members of the U.S. botanical community have played an important role in the development and shaping of systematic research and systematic institutions in developing countries. However, the relationships between botanists and developing countries are changing, and now should, and typically do, involve a partnership arrangement.

All the core programs in DEB fund research in foreign locales, but these may or may not involve foreign scientists and scientific infrastructural development of the host nation. Two programs at the Foundation, however, explicitly encourage this particular level of international involvement. Biotic Surveys & Inventories (NSF, 1990d) urges such an interaction between the U.S. and the foreign scientists, if the proposal involves research in a developing country. Most reviewers of BS&I proposals hold the PI accountable for the degree and level of involvement for such projects. Although expected in most such proposals, this activity is required for the research to be considered for funding through Biodiversity in Developing Countries (BDC) that is jointly supported by NSF and A.I.D. In its first two years, BDC funded 37 projects in 19 countries (Table 4). A.I.D. funds can be used only to support host country scientists and infra-

structure, title to any purchased equipment must remain in-country at the close of the award period, and all awards are subject to the principles that guide A.I.D. (Table 5). Counterpart NSF funds support the U.S. scientists' participation in the projects. A similar situation occurs for the program concerned with conservation of biodiversity, development of pharmaceuticals, and economic condition in third-world countries. This program is jointly funded by NSF, A.I.D., and the National Institutes of Health (NIH et al., 1992; Schweitzer et al., 1991).

International Programs at NSF also promotes international interactions. In my judgment, this program is under-utilized by the community of Systematic Biologists as a possible funding source.

## PRESENTATION OF SYSTEMATIC BIOLOGY TO THE GENERAL PUBLIC

NSF funds meritorious proposals for the transfer of scientific knowledge and ideas to society-at-large. One means of accomplishing such a transfer is to couple scientific studies with formal and/or informal educational programs. This combination of basic science and education may be proposed in single, successive, or concurrent proposals (NSF, 1988a, b). Thus, systematists might propose exhibits or lecture-series that explain systematic biology as a scientific discipline and that use the results of a funded project.

Systematic biology is in an ideal position to take advantage of any such funding opportunities because of the extensive interactions between natural history museums and herbaria and systematists. Museums and herbaria have received NSF support for development of instructional materials for classroom use and participation in teacher training efforts. Too often, however, these efforts have been conceived and proposed by non-scientists from public education offices without direct input from evolutionary biologists or systematists.

## SUMMARY

NSF funds most basic U.S. research in systematic biology and acts as an intellectual broker at various junctures in the chain of events that lead from the germinal idea for a research effort to the formulation of formal and rigorous inferences. However, the Foundation is not a direct player in the formal release of the data and conclusions that result from funded projects. Nevertheless, the Foundation can act as a knowledge broker in the funding of international and educational grants.

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# REVISED CIRCUMSCRIPTIONS AND SUBGENERIC TAXONOMIES OF *CALANDRINIA* AND *MONTIOPSIS* (PORTULACACEAE) WITH NOTES ON PHYLOGENY OF THE PORTULACACEOUS ALLIANCE[1]

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## Abstract

Cladistic analysis of Portulacaceae supports a revised taxonomy of *Calandrinia* sensu lato. *Calandrinia*, as here circumscribed, comprises ca. 14 western American species in three sections: *Calandrinia*, *Acaules*, and *Monocosmia*. Previous taxonomies classified over 100 species in *Calandrinia* but recognized *Monocosmia* as a distinct genus. *Calandrinia* sects. *Calandrinia* and *Monocosmia* are probably cladistically nested in section *Acaules* and are not sister groups of either *Rumicastrum* or *Montia*, as proposed in a previous cladistic analysis. *Montiopsis* Kuntze, traditionally included in *Calandrinia*, comprises ca. 15 western South American species in two subgenera, *Montiopsis* and *Dianthoideae*. At present, cladistic analysis provides only weak evidence linking *Calandrinia* and *Montiopsis* to one another and poorly resolves their precise relationships to other Portulacaceae. This analysis supports a taxonomic distinction between the eastern American/African and western American members of Portulacaceae, but poorly resolves the relationship between the two groups. Cactaceae, Basellaceae, Didiereaceae, and perhaps Hectorellaceae, which were not included in the analysis, belong to the eastern American/African group. The present analysis provides a framework for additional studies of phylogeny of the portulacaceous alliance and of Centrospermae in general.


*Calandrinia* Kunth, in its broadest circumscription, comprises more than 100 perennial and annual herbaceous species in western North America, western South America, and Australia, and represents the most diverse genus in the family (cf. Carolin, 1987, in press; Hershkovitz, 1990a, 1991a, b; Kelley, 1973; McNeill, 1974; Nyanyano, 1986a, 1990; Pax & Hoffmann, 1934; von Poellnitz, 1934a). Considerable evidence has emerged that *Calandrinia* sensu lato is an unnatural genus (Carolin, 1987; Hershkovitz, 1990a, 1991a), although differences in opinion remain regarding its taxonomy (Table 1) and the phylogenetic relationships of its constituent taxa to one another and to other Portulacaceae. As part of a continuing effort to clarify phylogeny in Portulacaceae, the primary aim of the present paper is to help establish natural circumscriptions of *Calandrinia* and its segregates. Because *Calandrinia* comprises such a phylogenetically divergent assemblage, however, the scope of this study encompasses all of Portulacaceae as well as the closely allied families Basellaceae, Cactaceae, Didiereaceae, and Hectorellaceae.

## Taxonomic History of *Calandrinia*

The traditional subgeneric and sectional taxonomy of *Calandrinia* was developed by Reiche (1897, 1898) and von Poellnitz (1934a) for the

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TABLE 1. Classification history of members of *Calandrinia* sensu lato and related taxa. Listed below are the generic and sectional assignments of members of *Calandrinia* sensu lato and other taxa regarded here as cladistically related (see also Carolin, 1987; Ford, 1992; Hershkovitz, 1990a, 1991a, 1992). The table compares traditional classifications with those adopted by Nyanyano (1986a, 1990), Carolin (1987, in press), and the present paper. The traditional classification synthesizes the taxonomy proposed by Añón (1953), Kelley (1973), Kelley & Swanson (1986), Mathew (1989), McNeill (1974), Pax & Hoffmann (1934), Peralta (1988), von Poellnitz (1934a), and Reiche (1897, 1898). This table lists only explicitly proposed synonymy. For example, Nyanyano included *Calandrinia axilliflora* as a species of *Calandrinia* sect. *Cistanthe*, but did not include *Calandrinia* sect. *Axillares* as a synonym of the latter (cf. Carolin, 1987, in press; Kelley, 1973; Reiche, 1897, 1898). The synonymy is not perfect, i.e., the assignment of particular species varies among the classifications, particularly in Nyanyano's (1986a) treatment. Except for *Rumicastrum* sect. *Basales*, the sectional assignments for the Australian calandrinias in Carolin's (1987) work depart markedly from those of von Poellnitz (1934; see also Syeda & Ashton, 1989). The more recent circumscriptions of the sections of *Rumicastrum* are accepted here uncritically. Reiche's (1897) subgeneric assignments of the sections of *Calandrinia* are indicated in parentheses. The nomenclatural authority is listed the first time each taxon is listed in the table.

| Traditional | Nyanyano | Carolin | Hershkovitz |
|---|---|---|---|
| *Calandrinia* (subg. *Hirsutae* Reiche) § *Hirsutae* Reiche | *Calandrinia* § *Calandriniopsis* Nyanyano, ined. | *Baitaria* § *Hirsutae* (Reiche) Carolin, ined. | *Montiopsis* Kuntze subg. *Montiopsis* |
| *Calandrinia* (*Hirsutae*) § *Condensatae* Reiche | *Calandrinia* Kunth § *Calandrinia* | *Baitaria* § *Condensatae* (Reiche) Carolin, ined. | *Montiopsis* subg. *Montiopsis* |
| *Calandrinia* (*Hirsutae*) § *Parviflorae* Reiche | *Calandrinia* § *Cistanthe* | *Baitaria* § *Condensatae* | *Montiopsis* subg. *Montiopsis* |
| *Calandrinia* (subg. *Glabrae* Reiche) § *Dianthoideae* Reiche | *Calandrinia* § *Calandrinia* | *Baitaria* § *Dianthoideae* (Reiche) Carolin, ined. | *Montiopsis* subg. *Dianthoideae* (Reiche) D. I. Ford |
| *Calandrinia* (*Glabrae*) § *Acaules* Reiche | *Calandrinia* § *Calandrinia* | *Baitaria* § *Acaules* (Reiche) Carolin, ined. (= *Baitaria* Ruiz & Pavón § *Baitaria*) | *Calandrinia* § *Acaules* |
| *Calandrinia* (*Glabrae*) § *Compressae* Reiche (= *C.* § *Calandrinia*) | *Calandrinia* § *Calandrinia* | *Calandrinia* sens. str. | *Calandrinia* § *Calandrinia* |
| *Calandrinia* (*Glabrae*) § *Axillares* Reiche | — | *Calandrinia* sens. str. | *Calandrinia* § *Calandrinia* |
| *Calandrinia* (*Glabrae*) § *Cistanthe* Reiche | *Calandrinia* § *Cistanthe* | *Cistanthe* § *Cistanthe* | *Cistanthe* § *Cistanthe* |
| *Calandrinia* (*Glabrae*) § *Arenariae* Reiche | *Calandrinia* § *Cistanthe* | *Cistanthe* § *Cistanthe* | *Cistanthe* § *Cistanthe* |
| *Calandrinia* (*Glabrae*) § *Rosulatae* Reiche | *Calandrinia* § *Calandrinia* | *Cistanthe* § *Cistanthe* | *Cistanthe* § *Cistanthe* |
| *Calandrinia* (*Glabrae*) § *Andinae* Reiche | *Calandrinia* § *Calandrinia* | *Cistanthe* § *Cistanthe* | *Cistanthe* § *Cistanthe* |
| *Calandrinia* (*Glabrae*) § *Amarantoideae* Reiche | *Calandrinia* § *Calandriniopsis* | *Cistanthe* § *Amarantoideae* (Reiche) Carolin, ined. | *Cistanthe* § *Amarantoideae* (Reiche) Carolin ex Hershkovitz |
| *Calandrinia* § *Basales* Poelln. | — | *Rumicastrum* § *Basales* (Poelln.) Carolin, ined. | *Rumicastrum* § *Basales* |
| *Calandrinia* § *Tuberosae* Poelln. | — | *Rumicastrum* § *Tuberosae* (Poelln.) Carolin, ined. | *Rumicastrum* § *Tuberosae* |
| *Calandrinia* § *Pseudodianthoideae* Poelln. | | *Rumicastrum* § *Pseudodianthoideae* (Poelln.) Carolin, ined. (= *Rumicastrum* Ulbr. § *Rumicastrum*) | *Rumicastrum* § *Rumicastrum* |

TABLE 1. Continued.

| Traditional | Nyanyano | Carolin | Hershkovitz |
|---|---|---|---|
| *Calandrinia* § *Apicales* Poelln. | — | *Rumicastrum* spp. | *Rumicastrum* spp. |
| *Calandrinia* § *Uniflorae* Poelln. | — | *Rumicastrum* spp. | *Rumicastrum* spp. |
| *Calandrinia* § *Pachypodeae* Kelley & Swanson | — | — | *Talinum* Adans. spp. |
| *Calandrinia* § *Partitae* Poelln. | — | — | *Anacampseros* § *Tuberosae* |
| *Calandrinia* § *Macrocarpae* Añón | *Calandrinia* § *Cistanthe* | *Schreiteria* Carolin | *Schreiteria* |
| *Calandriniopsis* E. Franz | *Calandrinia* § *Calandriniopsis* | *Baitaria* § *Condensatae* | *Montiopsis* subg. *Montiopsis* |
| *Montiopsis* Kuntze | *Montiopsis* | *Baitaria* § *Condensatae* | *Montiopsis* subg. *Montiopsis* |
| *Calyptridium* Nutt. | *Calyptridium* | *Calyptridium* | *Cistanthe* § *Calyptridium* (Nutt.) Hershkovitz |
| *Spraguea* Torr. | *Calyptridium* | *Calyptridium* | *Cistanthe* § *Calyptridium* |
| *Philippiamra* Kuntze (*Silvaea* Phil. non Hook. f. & Arn. ex Baillon) | *Philippiamra* | *Cistanthe* § *Amarantoideae* | *Cistanthe* § *Philippiamra* (Kuntze) Hershkovitz |
| *Monocosmia* Fenzl | *Calyptridium* | *Monocosmia* | *Calandrinia* § *Monocosmia* (Fenzl) Hershkovitz |
| *Lewisia* § *Strophiolum* B. Mathew | — | | *Cistanthe* § *Strophiolum* (B. Mathew) Hershkovitz |

American and Australian species, respectively. Reiche (1897) recognized two subgenera (*Glabrae* and *Hirsutae*) and 12 sections of *Calandrinia* in Chile (Table 1). Reiche (1902; cf. 1897, 1898) assigned the type species, *C. caulescens* Kunth (= *C. ciliata* (Ruiz & Pavón) DC), to *C.* (*Glabrae*) sect. *Compressae* (thus, sect. *Calandrinia*). Reiche's system was later extended, implicitly or explicitly, to cover extra-Chilean American species by Añón (1953), Kelley (1973), MacBride (1937), and Peralta (1988). Two additional American sections of *Calandrinia*, sections *Macrocarpae* (Añón, 1953) and *Pachypodeae* (Kelley & Swanson, 1986), were later proposed to accommodate species that did not correspond to any of Reiche's sections. These new sections were not assigned to subgenera. Also, *Montiopsis* Kuntze and *Calandriniopsis* Franz were established on the basis of species referable to subgenus *Hirsutae* (Carolin, in press; Ford, 1992). *Montiopsis* was accepted by Pax & Hoffman (1934) and Nyanyano (1986a, 1990) but was not mentioned by Carolin. *Calandriniopsis* was accepted by Pax & Hoffmann (1934), but not by Añón (1953), Nyanyano (1986a, 1990), or Carolin (in press).

The Australian calandrinias were classified in six sections by von Poellnitz (1934a; see Table 1). One of the sections (sect. *Partitae*) is actually synonymous with *Anacampseros* sect. *Tuberosae* (Carolin, 1987: 410; not mentioned by Gerbaulet, 1992). The other sections remained in taxonomic limbo for many years: they were subsequently referred to merely as the Australian calandrinias (Kelley, 1973; Pax & Hoffmann, 1934) and were never fully integrated into Reiche's (1897) subgeneric classification. Thus, a later "cladistic analysis of *Calandrinia*" (Syeda & Ashton, 1989; see also Syeda & Carolin, 1990) included only the Australian species, while a revision of the sectional taxonomy of *Calandrinia* (Nyanyano, 1986a; see also below) referred only to the American sections.

Within the last six years, three workers have proposed revised supraspecific classifications of all or part of *Calandrinia* sensu lato (Table 1), including Nyanyano (1986a, 1990), Carolin (1987, in press), and Hershkovitz (1990a, b, 1991a–c).

Syeda & Ashton (1989) and Syeda & Carolin (1990) did not formally propose a revised sectional taxonomy of the Australian species based on their cladistic analysis. Their analysis will not be considered in detail here except in reference to their data, much of which was incorporated in Carolin's (1987) work.

Nyanyano's (1986a, 1990) treatment most closely follows the traditional classification but is unsatisfactory especially because each of the three sections of *Calandrinia* sensu lato he circumscribed includes species with traits contrary to the sectional diagnoses. For example, Nyanyano (1986a) characterized section *Calandriniopsis* as pubescent, yet included therein the glabrous *Calandrinia* sect. *Amarantoideae* (cf. Hershkovitz, 1991b; Kelley, 1973); and characterized section *Cistanthe* as glabrous, yet included therein the pubescent *Calandrinia* sect. *Parviflorae* (cf. Ford, 1992; Hershkovitz, 1993; Kelley, 1973). Also, contrary to the states found in many of the included species, Nyanyano's (1986a) generic key diagnosed *Calandrinia* sensu lato as having 5–10 stamens and no tricolpate pollen (cf. Kelley, 1973), and his tribal key to Portulacaceae (Nyanyano, 1990) diagnosed Calandrineae as pubescent, perennial herbs or shrubs, and thus misrepresents the glabrous and/or annual members (cf. Kelley, 1973; Pax & Hoffmann, 1934; Reiche, 1898). Finally, Nyanyano (1986a) failed to mention the Australian sections of *Calandrinia* sensu lato, as well as several American taxa, in his treatment.

In his cladistic analysis of Portulacaceae, Carolin (1987) assigned the 18 traditionally recognized sections of *Calandrinia* sensu lato (excluding sects. *Partitae* and *Pachypodae*, which belong to other genera—see Table 1; Hershkovitz, 1991c) among 11 OTUs that, in his analysis, showed cladistic relationships with several different genera of Portulacaceae. Carolin concluded that *Calandrinia* sensu lato was not monophyletic and proposed restricting its generic circumscription to include only section *Calandrinia* (including sect. *Axillares*; Table 1). In his shortest cladogram (1987, fig. 7), *Calandrinia* sensu stricto is a sister group to the monotypic genus *Monocosmia*; these are, in turn, a sister group to the Australian calandrinias. Carolin preferred a slightly longer cladogram in which *Calandrinia* sensu stricto + *Monocosmia* is a sister group to his OTU *Naiocrene* (*Montia* sensu McNeill, 1975); he attributed the additional length of his preferred cladogram to character state changes that might be morphologically correlated. He concluded that the relationships of the *Calandrinia* sensu stricto + *Monocosmia* clade were unresolvable without additional study. Carolin (1987, in press) recommended assigning other members of *Calandrinia* sensu lato variously to *Cistanthe*, *Baitaria*, *Rumicastrum*, and *Schreiteria* (Table 1).

In previous papers, I discussed Carolin's (1987) work in the light of additional evidence from leaf morphology (Hershkovitz, 1990a, 1991a, b, 1992, 1993). I corroborated Carolin's opinion that *Calandrinia* sensu lato is unnatural and should be segregated into several genera. I adopted Carolin's proposal to classify four of Reiche's (1897) *Calandrinia* sections and the genus *Philippiamra* (syn. *Silvaea*) in *Cistanthe* (Table 1). My classification of *Cistanthe* departed from Carolin's in segregating *Cistanthe* sect. *Philippiamra* from section *Amarantoideae* and in recognizing *Calyptridium* (including *Spraguea*) and the monotypic *Lewisia* sect. *Strophiolum* as sections of *Cistanthe* (Table 1). I tentatively accepted Carolin's proposed circumscriptions of *Rumicastrum* and *Schreiteria*, but I presented evidence that the *Calandrinia* sensu stricto + *Monocosmia* clade is most closely related to and possibly nested within *Calandrinia* sect. *Acaules*, which Carolin referred to *Baitaria* (Table 1). Hence, I advocated including *Monocosmia* (see also Hershkovitz, 1991c) and *Baitaria* in *Calandrinia*, although I found no unequivocal evidence linking section *Acaules* with the other members of *Baitaria* sensu Carolin (i.e., *Calandrinia* sect. *Dianthoideae* and subg. *Hirsutae*; Table 1). In the present paper, I treat the last two as *Montiopsis* subgenera *Dianthoideae* and *Montiopsis*, respectively (Table 1).

## Phylogenetic Reanalysis of the Relationships among Members of *Calandrinia* sensu lato

My earlier taxonomic conclusions on *Calandrinia* sensu lato employed cladistic concepts but no formal numerical analysis other than preliminary McClade (Maddison & Maddison, 1987) manipulations of data modified from Carolin's (1987). I provide here a more extensive numerical analysis of Portulacaceae that aims primarily to clarify the circumscription and relationships of members of *Calandrinia* sensu lato. This work synthesizes my earlier reinterpretation (Hershkovitz, 1990a) of several characters included in Carolin's (1987) analysis, new evidence from leaf morphological studies (Hershkovitz, 1990a, 1991b, 1993), and additional character analyses as noted in Appendix

1. This analysis falls far short of a comprehensive revised phylogeny of Portulacaceae, especially because this family is probably paraphyletic with respect to Basellaceae, Didiereaceae, Hectorellaceae, and Cactaceae (see discussion). Along with Portulacaceae, these families constitute what I call the portulacaceous alliance (Hershkovitz, 1991d; "portulaca alliance" of Gibson & Nobel, 1986; Portulacineae of Thorne, 1976, 1983). Also, data for the poorly known genera *Talinella* (see Nyanyano, 1986b) and *Amphipetalum* (see Spichiger, 1988) remain to be incorporated, and a new genus, *Xenia*, was segregated from *Anacampseros* (Gerbaulet, 1992; see also below) while this manuscript was in review. Except for Hectorellaceae (see Skipworth, 1961), however, there is no evidence that the excluded taxa are especially close relatives of *Calandrinia*. The excluded taxa appear to be related to eastern American/African members of Portulacaceae, whereas members of *Calandrinia* sensu lato except for section *Macrocarpae* (Carolin, 1987) and the Australian endemics, seem to be related to western American Portulacaceae (Hershkovitz, 1990a, 1991a, d; cf. Carolin, 1987; see also discussion). My assumption, at this point, is that neither the eastern American/African nor western American group is polyphyletic, and that one group effectively provides an outgroup or set of outgroups for the other. Excluding phenetically distinctive members of the eastern American/African group will not prevent at least partial recovery of phylogenetic information pertinent to *Calandrinia* sensu lato, although ultimately a more thorough analysis will be necessary. Another problem with the present analysis is that while Portulacaceae and allies are clearly members of the order Centrospermae, their position in the order, hence the polarity of many of their variable characters, remains uncertain (Hershkovitz, 1989, 1991d; cf. Rodman et al., 1984; Carolin, 1987).

## Materials and Methods

*1. Taxa.* The 33 OTUs (excluding a hypothetical ancestor) recognized in the present analysis (Table 2) are substantially the same as Carolin's (1987) but with changes and precautions described below.

I treated *Rumicastrum*, *Claytonia*, and *Lewisia* as single OTUs based on Carolin's (1987) finding that each is monophyletic. Even if monophyletic, *Lewisia* is problematic because of its polymorphism and poorly correlated character states among the species (Hershkovitz, 1992). I will reconsider this problem in my discussion of the results.

Although Carolin (1987) determined that *Montia* is monophyletic, I treated section *Naiocrene* (1–2 spp.; McNeill, 1975) as a distinct OTU. Because it includes the only rosettiform perennial species of *Montia*, section *Naiocrene* possibly represents the basalmost clade in the genus. This section possesses traits that are otherwise discordant

Table 2. Taxa for cladistic analysis. Listed below are the full names of the OTUs recognized in the present analysis. The circumscriptions of the taxa are as proposed by Carolin (1987, in press) except where modified by Hershkovitz (see Table 1). Four taxa (*Montiopsis* subg. *Montiopsis*, *Claytonia*, *Rumicastrum*, and *Lewisia*) split for analytical purposes by Carolin (1987) are here lumped because Carolin determined that each is monophyletic. Traditional synonyms of autonyms are listed.

*Anacampseros* L. sect. *Anacampseros* (≡ *A.* § *Telephiastrum* (Medik.) Fenzl)
*Anacampseros* sect. *Avonia* E. Mey. ex Fenzl
*Anacampseros* sect. *Tuberosae* von Poelln.
*Calandrinia* Kunth sect. *Calandrinia* (≡ *C.* sect. *Compressae* Reiche)
*Calandrinia* (*Acaules*) *acaulis* Kunth
*Calandrinia* (*Acaules*) *affinis* Gillies ex Arn.
*Calandrinia* (*Acaules*) *caespitosa* Gillies ex Arn.
*Calandrinia* (*Acaules*) *carolinii* Hershkovitz & Ford
*Calandrinia* (*Acaules*) *compacta* Barnéoud
*Calandrinia* sect. *Monocosmia* (Fenzl) Hershkovitz
*Calyptrotheca* Gilg
*Ceraria* Pearson & Stephens
*Cistanthe* Spach sect. *Cistanthe*
*Cistanthe* sect. *Amarantoideae* (Reiche) Carolin ex Hershkovitz
*Cistanthe* sect. *Calyptridium* (Nutt.) Hershkovitz
*Cistanthe* sect. *Philippiamra* (Kuntze) Hershkovitz
*Cistanthe* sect. *Strophiolum* (B. Mathew) Hershkovitz
*Claytonia* L.
*Grahamia* Gillies ex Hook. & Arn.
*Lenzia* Phil.
*Lewisia* Pursh
*Montia* L., except section *Naiocrene*
*Montia* sect. *Naiocrene* (Torrey & A. Gray) Pax & K. Hoffm.
*Montiopsis* Kuntze subg. *Montiopsis*
*Montiopsis* subg. *Dianthoideae* (Reiche) D. I. Ford
*Portulaca* L.
*Portulacaria* Jacq.
*Rumicastrum* Ulbr.
*Schreiteria* Carolin
*Talinaria* Brandegee
*Talinopsis* A. Gray
*Talinum* Adans. sect. *Talinum* (≡ *T.* sect. *Talinastrum* DC.)
*Talinum* sect. *Phemeranthus* (Raf.) DC.

in *Montia*, however, including brachytetracytic stomata and a chromosome base number of 11 (see Appendix 1). Thus, treating *Montia* as a single OTU scored for the character states of section *Naiocrene* is problematic.

As noted above, I assigned *Calandrinia* sect. *Dianthoideae* and subgenus *Hirsutae* to *Montiopsis* subgenera *Dianthoideae* and *Montiopsis*, respectively. My choice of subgeneric rank for these entities permits recognition of Reiche's (1897, 1898) sectional divisions of subgenus *Montiopsis*. Reiche divided this subgenus into *Calandrinia* sects. *Hirsutae* (perennials), *Condensatae* (robust annuals), and *Parviflorae* (diminutive annuals); these circumscriptions are at least partially artificial (Ford, 1992).

The OTUs for *Cistanthe* are the sections I have recognized elsewhere (Table 1). Except for the addition of *C.* sect. *Strophiolum*, these correspond to Carolin's OTUs for the equivalent taxa.

My previous analysis (Hershkovitz, 1990a) indicated that the apparent cladistic affinities of *Calandrinia* sects. *Calandrinia* and *Monocosmia* might vary depending on how *Calandrinia* sect. *Acaules* was scored for its variable traits. No species of section *Acaules* has the entire suite of traits that I had earlier cited as evidence linking this section with section *Calandrinia*. Hence, I treated as independent OTUs five putative species of section *Acaules* (Hershkovitz, 1993) possessing different combinations of character states.

I have retained Carolin's two OTUs for *Talinum*, but they may be unsatisfactory for phylogenetic analysis. Elsewhere, three (Pax & Hoffmann, 1934) or four (Nyanyano, 1986a) subdivisions of *Talinum* have been recognized, and it is not clear how Carolin would have assigned these to his two sections. Specifically, Carolin (in press) divided *Talinum* into section *Phemeranthus* (enveloping seed aril present; ca. 25 spp.) and section *Talinum* (enveloping seed aril absent; ca. 6 spp.). *Talinum* group "B" of Pax & Hoffmann (1934: 249), more or less equivalent to "sect. *Concentricum*" of Nyanyano (1986a), includes up to 16 species that apparently lack the enveloping aril (Nyanyano, 1986a) but, in other respects, span the morphological extremes between the broad-leaved, diffusely branched species typifying section *Talinum* and the terete-leaved, rosettiform species typifying section *Phemeranthus*. I cannot account for these species in the context of Carolin's classification, but I leave this problem unresolved.

In addition to the above, I have previously discussed possible paraphyly among the sections of *Cistanthe* (Hershkovitz, 1991a). Other candidates for paraphyletic OTUs include *Calandrinia* sect. *Calandrinia* and *Montiopsis* subg. *Dianthoideae* (Hershkovitz, 1990a), in which other OTUs may be nested. For the present analysis, I retained these phenetically distinct but possibly paraphyletic OTUs but will reconsider the specific consequences in the discussion. The potential pitfalls of paraphyly would best be avoided by species-level analysis of the family, which is beyond the scope of the present study.

*2. Outgroup.* The outgroups of Portulacaceae or, more appropriately, the portulacaceous alliance, are unknown (Hershkovitz, 1989, 1990a, 1991a, in prep.; cf. Carolin, 1987; Rodman, 1990; Rodman et al., 1984); hence most character state polarities cannot be established by the two-outgroup method proposed by Maddison et al. (1984). In the present analysis, I designated a hypothetical ancestor scored as "0" for 28 of the 46 total characters with the balance scored as unknown. The character state polarities were subjectively determined on the basis of state distributions among other Centrospermae, which presumes that the portulacaceous alliance is derived therein (but see Hershkovitz, 1989).

*3. Characters.* Appendix 1 lists 46 mostly binary characters and data sources, and Table 3 lists the OTU scores. A few of the characters are multi-state/unordered. A "0" is entered for all states designated as ancestral a priori and, for convenience, states determined to be primitive a posteriori. Otherwise, the state designations are arbitrary.

I did not follow infrageneric analyses published elsewhere to derive scores for *Rumicastrum* or the OTUs of *Anacampseros*. Contrary to OTU scores I adopt here, Syeda & Ashton (1989) and Syeda & Carolin (1990) presumed that such traits as inaperturate pollen and numerous carpels are primitive in *Rumicastrum* (see Appendix 1). Some scores indicated in Gerbaulet's (1992) *Anacampseros* analysis, published while this manuscript was in review, are contrary to those adopted here. I have attempted to note all discrepancies in Appendix 1. Because Gerbaulet's results are generally consistent with those here and also because *Anacampseros* is phylogenetically relatively distant from *Calandrinia* and *Montiopsis*, I did not reanalyze using Gerbaulet's scores.

Infrataxon variation was problematic in scoring many OTUs (Table 3). I attempted to score variable OTUs for the presumed primitive state. In some

cases, I scored variable OTUs for the derived state of a polarized character, especially where I suspect that the "primitive" state is secondary. For example, I scored *Rumicastrum* for having tuberous roots—the putatively derived state in Portulacaceae—even though most species are not tuberous. Tubers in *Rumicastrum* occur in perennial species (Pate & Dixon, 1982; West, 1986), however, which I presume to be primitive with respect to the annuals, although this has not been demonstrated, specifically, in *Rumicastrum* (see, e.g., Syeda & Carolin, 1990). I used an approach suggested by Nixon & Davis (1991), viz, dividing polymorphic entities into monomorphic OTUs, to alleviate variation problems in *Calandrinia* sect. *Acaules* and, to a lesser extent, in *Montia* (see above). Nevertheless, infra-OTU variation remains for one or more characters (nine in *Portulaca*) in 18 of 33 OTUs, and character variation in other Centrospermae is also problematic in my consideration of ancestral states (see Appendix 1). I hope to be able to solve these problems in follow-up analyses. At this point, I just emphasize that such variation exists and note where it might affect the results.

Many workers (e.g., Doyle & Donoghue, 1986; Nixon & Davis, 1991; Sanderson & Donoghue, 1989) have recognized that cladistic analyses incorporating missing data scores can be misleading because the data, if available, might yield alternative results. Nevertheless, Table 3 includes three sorts of missing data scores, all scored as unknown ("?") in the parsimony program (see below). These include instances where the character state presumably exists in the OTU but has not been adequately or at all investigated ("?" in Table 3); where infrataxon variation prohibits a defensible scoring decision for the entire OTU ("V" in Table 3); and where "X" characters (Doyle & Donoghue, 1986) are employed.

Doyle & Donoghue (1986) devised "X" characters in order to reduce biases in inter-OTU distances where some OTUs lack a particular character that has two or more unpolarizable states. For example, they used "X" scoring for seed shape because radially and bilaterally symmetrical seeds are plausibly derivable from one another, as well as from the seedless condition, by a single evolutionary step. A three-state ordered transformation series was not justifiable, and simply using three unordered states (i.e., seeds absent/radiospermic/platyspermic) would bias against the homology of seed presence per se. Treating the different seed types as independent binary characters (i.e., seeds radiospermic vs. not and seeds platyspermic vs. not) would necessitate two steps in the derivation of one type from the other. Doyle & Donoghue treated seed presence/absence as one character and seed shape as another, with seedless taxa scored as unknown ("X") for the latter. In the present analysis, I adopted "X" scoring for leaf fimbrial vein anatomy (char. 14), stomatal subtype (char. 16), trichome ribbing (char. 21), the derivation of solitary flowers (chars. 22, 23), bract morphology (char. 26), capsule valve morphology after dehiscence (char. 41), and chromosome base numbers when other than nine (char. 46).

In addition to uncertain polarities and missing scores, continuous, rather than discrete, character state variation poses a problem for the present analysis (see Stevens, 1991). Indeed, some of the character states here recognized as different, e.g., petal numbers five, rarely six, versus usually more than five, blatantly overlap. Other states merely intergrade, but the scores reflect consistent distinctions between taxa. For example, in Portulacaceae as a whole, festooned brochidodromous leaf venation (char. 12) intergrades with brochidodromous, which intergrades with other venation patterns (see Hershkovitz, 1990a, 1991a, 1992, 1993). The distribution of this trait in the cladograms must be evaluated with the variation in mind. I emphasize that the scores employed here represent approximations or, in effect, hypotheses of actual character state differences that must eventually be validated by the sort of analyses proposed by Stevens (1991).

*4. Analysis.* I analyzed the Table 3 data matrix using PAUP 3.0r (Swofford, 1991) on a Macintosh Classic II computer with 6 megabytes of memory (RAM) plus "Virtual RAM" (VRAM). I allotted 4.5 and 8.5 kilobytes of memory to PAUP for use without and with VRAM, respectively, and set MAXTREES at 9,000–10,000 and 17,000–22,000 for the lower and higher memory allotments, respectively. I found that, with my hardware, increasing the number of trees in memory beyond 18,000 slows PAUP beyond practical functionality.

For all searches, I used MULPARS, Lundberg rooting, and the designated ancestral states (ANCSTATES) options. By including the ancestor in the search parameter, I generated rooted trees. As recommended by Swofford (1991), I used a variety of PAUP's customizable search modes to facilitate parsimony analysis. The options include taxon addition sequences that vary the configuration and length of the initial tree and "heuristic" branch-

TABLE 3. Data matrix for Portulacaceae. Characters and states are described in Appendix 1. Question marks denote missing, incomplete, or uninterpretable data. A "V" denotes that the character is too variable in the taxon to score with confidence. An "X" denotes a missing character, rather than missing data (see text). Underlined scores indicate infrataxon variability encompassing two or more states.

| OTU | 05 | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|
| Ancestor | ??000 | 00??? | 0?0X? | 0???? | X?000 | 00000 | 0?000 | ??000 | 00000 | X |
| *Anacampseros* § *Anacampseros* | 00001 | 10001 | 000X1 | 01000 | 01100 | 01001 | 00000 | 11111 | 00110 | X |
| *Anacampseros* § *Avonia* | 00001 | 10001 | ?00X1 | 00000 | X1100 | 01001 | 00000 | 11111 | 00110 | X |
| *Anacampseros* § *Tuberosae* | 01011 | 00001 | ?00X1 | 01000 | X1100 | 01001 | 00000 | 00111 | 00110 | X |
| *Calandrinia acaulis* | 01000 | 00110 | 00100 | 10000 | X1X10 | 00001 | 10000 | 00000 | 0000? | ? |
| *Calandrinia affinis* | 01000 | 00110 | 00100 | 11000 | 11X11 | X0011 | 10000 | 00000 | 00001 | ? |
| *Calandrinia caespitosa* | 01000 | 00110 | 000X0 | 11000 | 11X11 | X0011 | 10000 | 00000 | 00001 | 2 |
| *Calandrinia carolinii* | 01000 | 00110 | 00100 | 11000 | 11X10 | 00011 | 10000 | 00000 | 0000? | ? |
| *Calandrinia compacta* | 01000 | 00110 | 000X0 | 01000 | 11X11 | X0001 | 10000 | 00000 | 0000? | ? |
| *Calandrinia* § *Monocosmia* | 01100 | 00110 | 00100 | 11000 | 11X11 | X0001 | 10100 | 00000 | X0001 | 1 |
| *Calandrinia* § *Calandrinia* | 01100 | 00110 | 00100 | 11000 | 11X11 | X0001 | 10000 | 00000 | 10001 | 2 |
| *Calyptrotheca* | 10000 | 0000? | ??0X1 | 00000 | X0000 | 000?1 | 1?010 | 10000 | 00000 | ? |
| *Ceraria* | 10010 | 01001 | 010X1 | 00000 | X0000 | 00000 | 00001 | 00000 | X0001 | 2 |
| *Cistanthe* § *Amarantoideae* | 01100 | 0011? | 110X0 | 00000 | X1100 | 10000 | 00000 | 00000 | 00001 | 0 |
| *Cistanthe* § *Calyptridium* | 01V00 | 0011? | 110X0 | 00000 | X1100 | 10000 | 00100 | 00000 | 00001 | 1 |
| *Cistanthe* § *Cistanthe* | 01000 | 0011V | 110X0 | 00000 | X1100 | 10000 | 00000 | 00000 | 00001 | 1 |
| *Cistanthe* § *Philippiamra* | 01100 | 0011? | 110X0 | 00000 | X1100 | 10000 | 00101 | 00000 | X000? | ? |
| *Cistanthe* § *Strophiolum* | 01000 | 0011? | 010X0 | 00000 | X1100 | 10010 | 00000 | 00000 | 00001 | ? |
| *Claytonia* | 01000 | 00110 | 00110 | 00000 | X1101 | X0000 | 00000 | 00000 | 11001 | V |
| *Grahamia* | 10011 | 1000? | 100X1 | 00000 | X1X10 | 00001 | 01000 | 11100 | 00110 | X |
| *Lenzia* | 01000 | 0011? | 000X0 | 00000 | X1X1? | ?0000 | 00000 | 00000 | 0000? | ? |
| *Lewisia* | 01000 | 00110 | 000X0 | 00000 | X1000 | 00110 | 01010 | 00000 | 00001 | V |
| *Montia* (excl. § *Naiocrene*) | 01000 | 00110 | 00110 | 00000 | X1101 | X0001 | 00000 | 00000 | 11001 | V |
| *Montia* § *Naiocrene* | 01000 | 00110 | 00110 | 10000 | X1101 | X0001 | 00000 | 00000 | 11001 | 1 |
| *Montiopsis* § *Dianthoideae* | 01000 | 00110 | 000X0 | 01111 | 01200 | 00000 | 00000 | 00000 | 00001 | 0 |
| *Montiopsis* § *Montiopsis* | 01000 | 00110 | 000X0 | 01111 | 01200 | 00001 | 10000 | 00000 | 00001 | 0 |
| *Portulaca* | 00V01 | 1V001 | 010X1 | 00000 | X0000 | 01001 | 01000 | 10100 | 00000 | X |
| *Portulacaria* | 10010 | 01001 | 000X1 | 00000 | X0000 | 00000 | 00001 | 00000 | X0001 | 1 |
| *Rumicastrum* | 01010 | 0000? | 100X? | 00000 | X1100 | 00001 | 00000 | 00000 | 0000? | ? |
| *Schreiteria* | 00010 | 0000? | 100X0 | 10000 | X1000 | 00101 | 10000 | 10100 | 0000? | ? |

TABLE 3. Continued.

| OTU | 05 | 10 | 15 | 20 | 25 | 30 | 35 | 40 | 45 | 46 |
|---|---|---|---|---|---|---|---|---|---|---|
| *Talinaria* | 00011 | 10001 | 000X1 | 00000 | X1100 | 01001 | 00000 | 11111 | 0011? | ? |
| *Talinopsis* | 00011 | 1100? | 100X1 | 00000 | X1000 | 00001 | 00000 | 11110 | 0011? | ? |
| *Talinum* § *Phemeranthus* | 01010 | 00001 | 100X1 | 00000 | X1000 | 01001 | 00000 | 00000 | 00101 | 2 |
| *Talinum* § *Talinum* | 00010 | 00001 | 110X1 | 01000 | 01000 | 01001 | 00000 | 11100 | 00001 | 2 |

swapping algorithms that vary the extent to which existing trees are modified in the search for new trees. The fastest algorithm, "nearest neighbor interchange" (NNI), rearranges branches locally, and hence it may not find shorter trees with radically different topologies. The slowest and most thorough heuristic algorithm, "tree bisection-reconnection" (TBR), rearranges trees radically in its search for shorter trees. Intermediate between these is "subtree pruning-regrafting" (SPR). I experimented with all three modes according to the objective of the particular search, but I found that SPR was dispensable for my purposes.

Other PAUP options used here include strict, semistrict, and majority-rule consensus tree computation, the last of which also produces a table of all clades and their frequency among all of the trees in memory; character change and apomorphy lists that output the character state changes occurring for all characters and at all internodes, respectively; the tree filter, which finds among the trees in memory those of particular lengths or topologies; search constraints, which search for trees of particular predefined topologies in any of the search modes; and "starting trees," which permits PAUP to swap on one or more specified trees. The specific utility of each of these options in the present study is described below in the results.

## RESULTS

From 100 replicates of rapid searches initiated using a random taxon addition sequence, variously TBR or NNI, and 30-tree limits, I found minimal length trees of 107 steps. The consistency index (CI) of 107-step trees is 0.449; the rescaled consistency index (RC; Farris, 1989) is 0.346. Because of the "missing data" scores and infra-OTU character variation, the actual CI and RC may be lower (Nixon & Davis, 1991; Sanderson & Donoghue, 1989). Using the present data, I filtered from ca. 29,000 previously saved trees over 11,000 107-step trees and none shorter. The ca. 29,000 trees had been generated using a slightly different data matrix. Entering the ca. 11,000 trees as starting trees, I used TBR to increase their number to over 15,000 107-step trees with over 13,000 remaining to swap. I then switched to NNI, which is faster but finds fewer of the possible equally parsimonious trees, and increased the number of trees to over 19,000, with over 14,000 remaining to swap. At this point, I aborted the search because, from previous experience using similar data sets, I found that such a ratio of trees saved/remaining is an indication that the total number of equally parsimonious trees is at least an order of magnitude

higher, in this case exceeding the memory capacity of both the hardware and the program. Moreover, with this large tree buffer, PAUP was swapping on less than two trees per minute.

In order to generate a reliable consensus tree given the memory limitation (i.e., to avoid an over-representation of particular topologies among the total number of trees), I initiated additional searches using TBR to completion constraining for two particular topologies that were rare among the ca. 19,000 as determined by the clade frequency table: a constraint for trees with *Claytonia* + *Montia* (2 OTUs) + *Lewisia* as outgroups to the remaining OTUs (in 43 of 19,000 trees), and one for trees with *Calandrinia acaulis* + *C. caespitosa* + *C. carolinii* forming a clade (38/19,000). These searches yielded a total of over 5,000 additional 107-step trees.

The strict consensus tree of the total ca. 24,000 107-step trees (saved in three files) is shown in Figure 1. The black, shaded, and diagonally hatched branches delineate the western American, eastern American/African, and Australian taxa, respectively (Hershkovitz, 1991a, fig. 3). Putative positions of Cactaceae, Basellaceae, Didiereaceae, and *Talinella* (see below) are indicated by dashed branches. The semistrict consensus tree topology (Bremer, 1990) generated from the 17,000-tree treefile was identical to the strict consensus. The consensus tree is not a phylogeny (Anderberg & Tehler, 1990; Maddison, 1989): its "length" is 114—seven steps longer than that of its completely bifurcate resolutions. It does show, however, which groups are monophyletic in all 24,000 rearrangements and all unambiguous consensus character state changes (i.e., excluding those dependent on the particular resolution). The transitions indicated in Figure 1 for characters 15 and 24 appear equivocal but are not: by using constrained searches such as those described below, I determined that resolutions consistent with alternative positions for these transitions do not occur among 107-step trees.

For reference, all character state changes determined using the accelerated transition (ACCTRAN) optimization are listed in Appendix 2. Collectively, Appendix 2 presents a distorted picture of character state evolution in Portulacaceae in that seven superfluous changes are indicated and many changes would appear differently using alternative optimizations. In one or more optimizations, characters not indicated on the consensus tree undoubtedly provide synapomorphies for one or more clades in any of the possible resolutions, e.g., fimbrial vein presence (char. 13) must support at least one subclade in any resolution within the *Calandrinia* clade. Because of the large number of trees, however, it is not practical to evaluate the character evidence for each permutation of the consensus. The various alternatives for ambiguous or equivocal character state changes not shown in Figure 1 are not all mutually compatible, i.e., the topology required to assign a particular character state change to a given node of the consensus tree effectively prohibits other changes from simultaneously occupying that node. I did not attempt to identify a permutation of the consensus tree that would resolve the largest number of ambiguities.

From the clade frequency matrices (not shown), I found a wide variety of resolutions of the polytomous nodes, but not all possible sister group relationships were evident. To determine which of the possible sister group relationships among the unresolved basal 5-tomy were compatible with 107-step trees, I initiated additional searches using appropriate constraints, TBR and/or NNI, a random addition sequence with 50 or more replicates, and 30-tree limits. Table 4 shows all compatible relationships and the length of the shortest trees found for incompatible groupings. Table 4 also shows minimal tree lengths generated when constraining for alternative sister group relationships of the *Calandrinia* clade, the *Montiopsis* clade, the *Calandrinia* + *Montiopsis* clade, the eastern American/African clade (see above; cf. Fig. 1), and the *Calandrinia* + *Montiopsis* + eastern group clade.

I used constrained topology searches in order to evaluate additional phylogenetic hypotheses, e.g., Carolin's (1987) results that showed *Calandrinia* sections *Calandrinia* and *Monocosmia* linked with *Rumicastrum* or *Montia* (see above). From more than 50 replicates using a random addition sequence and NNI, I found minimal length trees of 116 and 111 steps, respectively, for the alternative relationships. Likewise, searches initiated using appropriate constraints to evaluate Carolin's (1987) result showing *Baitaria* as monophyletic generated minimal length trees of 110 steps. I have previously suggested that *Calandrinia* sect. *Acaules* is paraphyletic with respect to sections *Calandrinia* and *Monocosmia*. Constraining for the monophyly of section *Acaules* generated 108-step trees. Constraining for a clade comprising all OTUs formerly assigned to *Calandrinia* sensu lato excluding those sections that were based on taxa belonging to other genera (e.g., sect. *Pachypodeae*) generated 122-step trees. Constraining for the monophyly of *Talinum* sects. *Talinum* and *Phemeranthus* (cf. Carolin, 1987) generated 109-step trees. Finally, be-

1

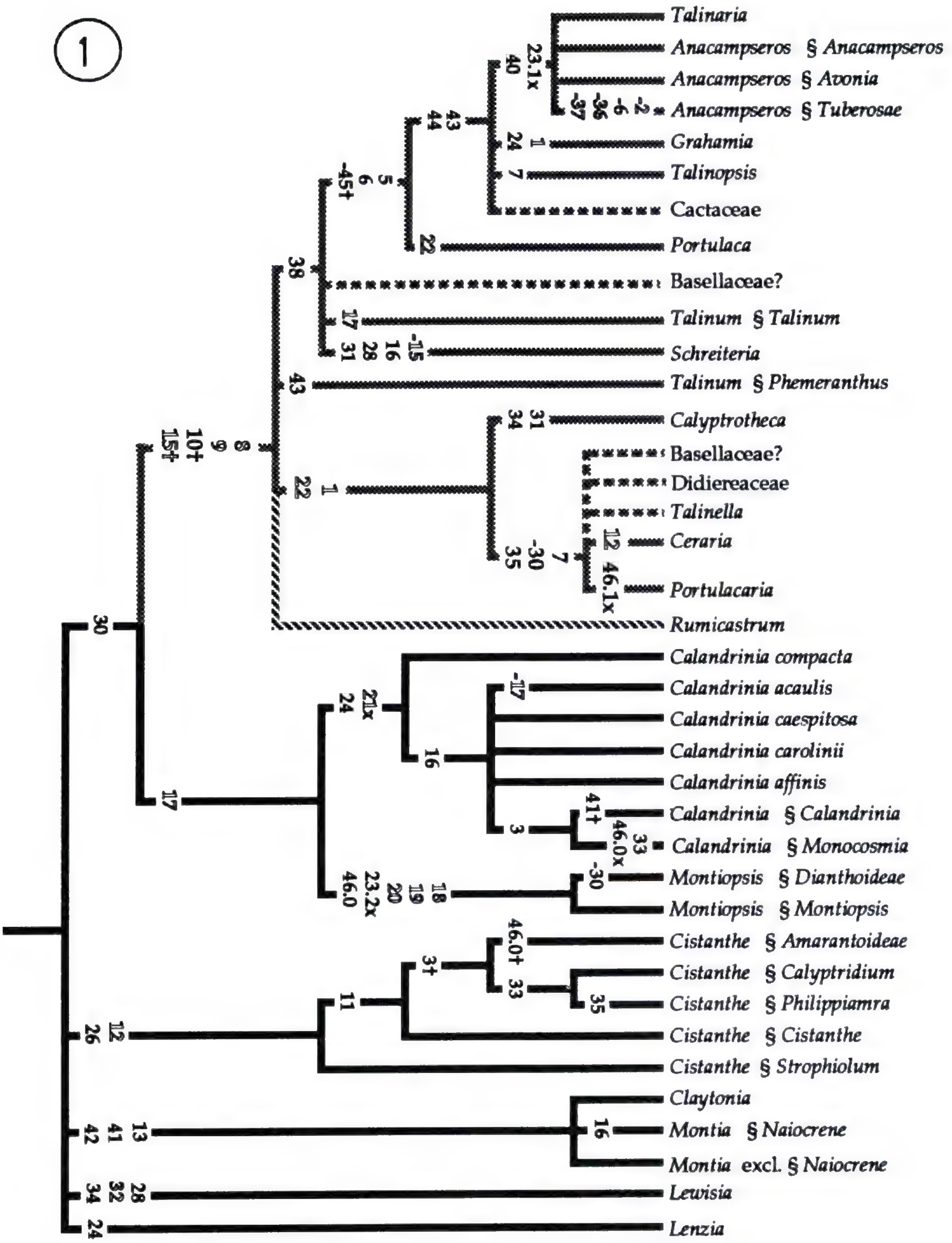


FIGURE 1. Consensus tree for Portulacaceae. Shown here is the consensus for 24,000 107-step cladograms found in the present phylogenetic analysis. The eastern American/African, Australian, and western American taxa are delineated by, respectively, gray shaded, diagonally hatched, and black branches. Taxa delineated by hyphenated branches were not included in the computer analysis, but were added in manually (see discussion). Unambiguous character state changes are shown on the branches (cf. Appendix 1). Polarized characters are shown in black, unpolarized characters are shown in white, and "x" and "†" denote characters scored as unknown ("X" character or missing value) for an OTU on an adjacent branch (cf. Table 3). The positions of the character 15 and 24 transitions appear equivocal but are consistent with all known 107-step resolutions of the tree.

TABLE 4. Sister group relationships compatible with 107-step trees. Denoted below by "+" are sister group relationships that occur among the 107-step trees found in the present analysis (cf. Fig. 1). The minimum length of trees with incompatible sister group relationships is also indicated. The generic taxonomy follows Table 2. The taxon designated "E. group" refers to the eastern American/African group of Portulacaceae (see text; cf. Fig. 1). "Ingroup minus taxon" refers to a sister group relationship between the indicated taxon and the remainder of Portulacaceae. In the case of the E. group, the ingroup is, effectively, a clade comprising the western American group (see text; cf. Fig. 1).

| | *Calandrinia* | *Montiopsis* | *Calandrinia* + *Montiopsis* | *Calandrinia* + *Montiopsis* + E. group | E. group | *Lewisia* | *Lenzia* | *Cistanthe* | *Claytonia* + *Montia* | Ingroup minus taxon |
|---|---|---|---|---|---|---|---|---|---|---|
| *Calandrinia* | ... | + | ... | ... | 108 | 109 | 111 | 110 | 108 | 108 |
| *Montiopsis* | | ... | ... | ... | 108 | 108 | 108 | 108 | 108 | 108 |
| *Calandrinia* + *Montiopsis* | | | ... | ... | + | 108 | 108 | 109 | 109 | 108 |
| *Calandrinia* + *Montiopsis* + E. group | | | | ... | ... | + | + | + | + | + |
| E. group | | | | | ... | 108 | 108 | 109 | 108 | 108 |
| *Lewisia* | | | | | | ... | + | 108 | 108 | + |
| *Lenzia* | | | | | | | ... | + | + | + |
| *Cistanthe* | | | | | | | | ... | + | 108 |
| *Claytonia* + *Montia* | | | | | | | | | ... | 108 |

cause Figure 1 shows two unambiguous reversals to tricolpate from panaperturate pollen (cf. Hershkovitz, 1989, 1991a), I constrained for trees showing the reversal to be at least equivocal. This search generated 108-step trees that are included among those showing the eastern American/African and western American groups as monophyletic (Table 4).

To summarize, for purposes of the present study, the most important results shown in Figure 1 include, first, evidence consistent with my earlier conclusions (Hershkovitz, 1990a, 1991a) that *Calandrinia* sects. *Calandrinia*, *Acaules*, and *Monocosmia* form a monophyletic group. Second, a single trait (trichome presence, char. 17) supports the sister group relationship between *Calandrinia* and *Montiopsis*, although the trichomes in the two genera are structurally distinct (Hershkovitz, 1993). In trees only one step longer, *Montiopsis* has at least six possible alternative sister groups (Table 4). Third, the consensus is consistent with Carolin's (1987) results indicating that *Calandrinia* sensu lato is unnatural and that *Cistanthe* is monophyletic. Fourth, the tree supports my proposal (Hershkovitz, 1991a, d) that the western American and eastern American/African Portulacaceae are phylogenetically set apart from one another. In this analysis, the latter appear to be monophyletic and the former paraphyletic but equivocally monophyletic in trees one step longer (Table 4).

## Discussion

Although the highly polytomous Figure 1 consensus tree might be dissatisfying for its lack of resolution, it serves the primary purpose of this study, which is to determine the relationships of Carolin's (1987) *Calandrinia* sensu stricto + *Monocosmia* clade and, in general, to advance taxonomic understanding of *Calandrinia* sensu lato. The results of this analysis also provide a framework for additional study of more precise relationships within the segregates of this genus, as well as among other Portulacaceae and Centrospermae.

### A. Taxonomy and Relationships of *Calandrinia* and *Montiopsis*

The consensus tree supports my earlier contention (Hershkovitz, 1990a) that *Calandrinia* sects. *Calandrinia* and *Monocosmia* are closely related to section *Acaules* and my hypothesis that the last is paraphyletic with respect to the first two. The paraphyly of section *Acaules* is evidenced by a single unambiguous character state change (presence of tetracytic/staurocytic stomata, char. 16) and, ambiguously, by another (fimbrial vein presence or subtype (chars. 13, 14). I also emphasize that section *Calandrinia* is possibly paraphyletic with respect to section *Monocosmia*. The only eligible autapomorphy for section *Calandrinia* (capsule-valve inrolling, char. 41) is nonuniversal (Appendix 1) and not readily evaluated in section *Monocosmia*.

While I believe that the results of the present analysis adequately evidence the monophyly of *Calandrinia*, I do not believe that a cladistic sectional taxonomy can be justified in the absence of a species-level analysis, especially because the functional OTUs employed here for section *Acaules* form a clade in trees only one step longer than the shortest. Because I am unable to offer anything cladistically more defensible, Carolin's (in press) circumscriptions of sections *Acaules* and *Calandrinia* (including sect. *Axillares*) are here retained.

Also consistent with my earlier conclusions (Hershkovitz, 1990a), the present analysis shows *Montiopsis* as monophyletic and linked only weakly with *Calandrinia*. The monophyly of *Montiopsis* is evidenced by its unique inflorescence (char. 23), assorted multicellular trichomes (chars. 18–20), and chromosome base number (char. 46). According to Figure 1, the reversal from panaperturate to tricolpate pollen provides an autapomorphy for subgenus *Dianthoideae*. I have previously noted (Hershkovitz, 1991a) that reversals from panaperturate to tricolpate pollen indicated in Carolin's (1987, fig. 7) cladogram (for subg. *Dianthoideae* and the *Portulacaria* + *Ceraria* clade) are actually equivocal. In the present analysis, both are unambiguous but become equivocal by allowing an additional step or, as I determined fortuitously, by scoring *Calandrinia caespitosa* for lacking trichomes. For this reason, and because there appears to be no precedent for such a reversal elsewhere among angiosperms, I hesitate to accept this trait as an autapomorphy or, without additional analysis, a phylogeny that requires such a reversal. Otherwise, I cannot document an autapomorphy for subgenus *Dianthoideae*, so the possibility that it is paraphyletic with respect to subgenus *Montiopsis* must be considered (see also below). Subgenus *Montiopsis* can be diagnosed on the basis of a unique trichome type that consists of elongated, intertwined cells (Ford, 1992; Hershkovitz, 1993; Kelly, 1973) and also, perhaps, on the basis of its pantoporate pollen.

As noted above, the sister group relationship between *Montiopsis* and *Calandrinia* is supported only by the shared presence of trichomes (char. 17), although the trichomes are structurally dis-

tinct. I have also noted leaf venation and epidermal similarities between *Montiopsis* and *Calandrinia* (Hershkovitz, 1993). Specifically, venation patterns in *Montiopsis* superficially resemble those in some species of *C.* sect. *Acaules* (although the similarity is in the shared lack of distinctive features) and tetracytic/staurocytic stomata occur in *M.* subg. *Dianthoideae*. Against the weak evidence favoring a *Montiopsis/Calandrinia* sister group relationship, however, there is also weak evidence to the contrary. In previous PAUP runs, I inadvertently scored *Calandrinia caespitosa* for lacking trichomes (although it is variable for this trait, and I scored it correctly for trichome morphology, char. 21). These searches generated the ca. 29,000 (108-step) trees from which the ca. 11,000 107-step trees were filtered using the corrected data (see above). In fact, the 29,000 trees in the earlier search probably represent only a small fraction of the total number of 108-step trees given that particular data file. In any case, with the single different score, all of the possible sister group relationships for *Montiopsis* indicated in Table 4 occurred among minimal length trees. This result renders the trichome evidence for a *Calandrinia* + *Montiopsis* sister group relationship even more tenuous because of its dependence on precise relationships and character state distributions in *Calandrinia* that cannot, at present, be adequately evaluated. I had previously been inclined to retain *Montiopsis* in *Calandrinia*, but given the relative homogeneity of each genus and the possibility that they are not closely related, their segregation seems warranted. Perhaps the only justification for retaining *Montiopsis* in *Calandrinia* would be if *M.* subg. *Dianthoideae* proved to be paraphyletic with respect to both *Calandrinia* and *M.* subg. *Montiopsis*. I have considered this possibility (Hershkovitz, 1990a). but it remains unscrutinized.

Figure 1 shows *Calandrinia* and *Montiopsis* together forming the sister group to the eastern American/African Portulacaceae evidenced by the shared derivation of panaperturate pollen. As I noted above, this sister group relationship is also contingent upon the homology of trichomes in *Calandrinia* and *Montiopsis*, and the relationship becomes equivocal in trees one step longer than minimal (Table 4). Among the 108-step trees are those showing a sister group relationship between *Calandrinia* and *Claytonia* + *Montia* (Montieae), reminiscent of Carolin's (1987) suggestion of a close relationship between *Calandrinia* (minus sect. *Acaules*) and *Montia*. The latter seems unlikely not only on parsimony grounds, but because either *Calandrinia* (sensu Hershkovitz) or Montieae must then be artificial. Nevertheless, a *Calandrinia*/Montieae relationship deserves additional scrutiny, especially because my data matrix presumes that putative similarities in inflorescence and fruit morphology in *C.* section *Calandrinia* and Montieae are not homologous (see Appendix 1).

See Table 5 for a synopsis of a revised sectional taxonomy of *Calandrinia* and *Montiopsis*.

### B. TAXONOMY AND RELATIONSHIPS OF OTHER MEMBERS OF *CALANDRINIA* SENSU LATO

Figure 1 confirms Carolin's (1987) general result that the remaining members of *Calandrinia* sensu lato are phylogenetically interspersed among several other traditional genera of Portulacaceae. My earlier proposed circumscription of *Cistanthe*, which includes members of *Calandrinia* sensu lato and three to four other traditional genera (Table 1), is upheld. The consensus of the infrasectional relationships differs from, but is not inconsistent with, what I suggested earlier (Hershkovitz, 1991a, fig. 3). Specifically, my earlier figure shows either section *Strophiolum* or *Cistanthe* as possible sister groups of the remainder of the genus. As I noted before, however, section *Cistanthe* is highly polymorphic and section *Amarantoideae* lacks an unequivocal autapomorphy; hence resolution of phylogeny within *Cistanthe* will necessitate a species-level analysis.

According to Figure 1, the remaining two members of *Calandrinia* sensu lato, *Rumicastrum* and *Schreiteria*, are members of the eastern American/African Portulacaceae and are not closely related to other members of *Calandrinia* sensu lato. *Rumicastrum* is rosettiform, however, and individual species possess leaf morphological features characteristic of *Cistanthe* (Hershkovitz, 1991b). Hence, I hesitate to conclude that its position in the consensus tree is correct. My results for *Rumicastrum* are difficult to compare with Carolin's (1987, fig. 7) because of overall topological differences in our respective trees. Nevertheless, ignoring the position of *Calandrinia* sects. *Calandrinia* and *Monocosmia* in Carolin's tree, the closest relatives of *Rumicastrum* and *Schreiteria* are members of the eastern American/African group. This result is not inconsistent with Figure 1.

The possibility that *Rumicastrum* (or *Rumicastrum* + *Talinum* sect. *Phemeranthus*, which occurs in some trees) is basal in the eastern American/African group may prove to be significant in resolving the problem of pollen evolution in Portulacaceae. To avoid the reversal to tricolpate pol-

TABLE 5. Key to and synopsis of the *Calandrinia* sections and *Montiopsis* subgenera. The diagnoses are based on data presented in Appendix 1 and Table 3.

A. *Calandrinia*
- 1a. Plants perennial, rosettiform, without leafy aerial stems; leaves glabrous or with unicellular-ribbed, sometimes papillate trichomes; flowers solitary, arising from basal leaf axils; stigmas 3 5; seeds several in a 3(–4)-valvate capsule . . . . . A2. *C.* sect. *Acaules*
- 1b. Plants annual, rosettiform, with leafy aerial stems arising from rosette axils; leaves usually with unicellular-ribbed, sometimes papillate trichomes, rarely truly glabrous; flowers arising variously from leafy, bracteate, or naked nodes of aerial stem, hence sometimes apparently racemose or paniculate; stigmas 2–3; seeds several in a 3-valvate capsule or 1–2 in a 2-valvate, incompletely dehiscent fruit.
  - 2a. Leaves probably always with (sometimes papillate) unicellular trichomes; flowers arising from axils of alternating leaves or bracts alternating with leaves on 0–1-branched aerial stems, hence sometimes apparently racemose; stigmas 3; seeds several in a 3-valvate capsule . . . . . A1. *C.* sect. *Calandrinia*
  - 2b. Leaves with papillate trichomes or glabrous; flowers arising variously and irregularly from leaf or bract axils or naked nodes on branched aerial stems, hence apparently paniculate; stigmas 2; seeds 1–2 in a 2-valvate, incompletely dehiscent achene-like fruit . . . . . A3. *C.* sect. *Monocosmia*

B. *Montiopsis*
- 1a. Plants perennial; multicellular trichomes variously uniseriate or multiseriate and glandular or eglandular (or rarely absent), but never formed by elongate, intertwined hair cells; pollen tricolpate . . . B1. *M.* subg. *Dianthoideae*
- 1b. Plants annual or perennial; multicellular trichomes variously uniseriate or multiseriate and glandular or eglandular, but trichomes formed by elongate, intertwined (sometimes barbed) hair cells always present; pollen pantoporate . . . . . B2. *M.* subg. *Montiopsis*

**A. Calandrinia** Kunth in HBK, Nov. Gen. Sp. 6: 77. 1823. nom. conserv. TYPE: *C. caulescens* Kunth (type conserv.; = *C. ciliata* (Ruiz & Pavón) DC.).

**A1. C.** sect. **Calandrinia.** About 5 spp. of temperate western America and montane southern Mexico, Guatemala, and temperate South America.

**A2. C.** sect. **Acaules** Reiche, Ber. Deutsch. Bot. Ges. 15: 500. 1897. TYPE: *C. acaulis* Kunth (lectotype, here designated). About 8 spp. of the Andes region, with one disjunct to southern Mexico.

**A3. C.** sect. **Monocosmia** (Fenzl) Hershkovitz, Phytologia 70: 223. 1991. TYPE: *C. monandra* (Ruiz & Pavón) DC. One species in Chile and Argentina.

**B. Montiopsis** Kuntze, Revis. Gen. Pl. 3(2): 14. 1898. TYPE: *M. boliviana* Kuntze (= *M. cumingii* (Hook. & Arn.) D. I. Ford).

**B1. M.** subg. **Montiopsis.** About 15 spp. of temperate western South America.

**B2. M.** subg. **Dianthoideae** (Reiche) D. I. Ford, Phytologia 74: 277 1993. TYPE: *M. cistiflora* (Gillies ex Arn.) D. I. Ford (lectotype, selected by Ford) About 3 spp. of temperate western South America.

len in trees as long as 108 steps, *Portulacaria* + *Ceraria* (± *Calyptrotheca*) must be the basal branch in the eastern American/African clade or *Portulacaria* + *Ceraria* must occupy the second most basal branch. Thus, with *Rumicastrum* occupying the basal branch, tricolpy is, at best, equivocally primitive in this group, and the number of topologies that permit tricolpy to be primitive is restricted.

## C. PHYLOGENETIC RELATIONSHIPS AMONG OTHER GENERA OF PORTULACACEAE

A thorough consideration of the relationships among Portulacaceae or, more appropriately, the portulacaceous alliance, is ultimately critical for resolving the precise relationships among members of *Calandrinia* sensu lato but is beyond the scope of the present paper. Nevertheless, the results of the present analysis are at least sufficient to compare with Carolin's (1987) results and to offer general conclusions.

Figure 1 supports my earlier notion (Hershkovitz, 1991a, b, d) of a phylogenetic partition between the fundamentally eastern American/African members of Portulacaceae and the western American and places the Australian endemic *Rumicastrum* in the former group. In trees one step longer, the eastern American/African and western American groups are each equivocally monophyletic (Table 4). Figure 1 can be compared with Carolin's (1987, fig. 8) area cladogram in which all of the minor clades he recognized except *Rumicastrum* can be assigned to eastern America/Africa or western America. Figure 1 also reproduces, albeit with less resolution, Carolin's clade "H," comprising *Portulaca*, *Talinopsis*, *Grahamia*, *Anacampseros*, and *Talinaria*. Gerbaulet (1992) discussed in detail monophyly and interrelationships among the last four genera ("*Ana-*

*campseros* group"; but see discussion of Cactaceae below). My results with respect to relationships within and proximal to the *Anacampseros* group would have differed using Gerbaulet's (1992) character data, but I suspect that the fundamental conclusions presented here (viz, the circumscription of *Calandrinia* sensu stricto, the eastern American/African vs. western American distinction, and even the relative position of the *Anacampseros* group) would remain. Figure 1 shows *Portulacaria* and *Ceraria* as sister groups, but this relationship has not been controversial (cf. Carolin, 1987, in press; McNeill, 1974; Nyanyano, 1989; Pax & Hoffmann, 1934; Rauh & Schölch, 1965).

Because of the potential problems in OTU delimitation, infra-OTU character variation, and character analysis, Figure 1 must be interpreted cautiously. For example, *Lewisia* comprises species with character combinations suggestive of other Portulacaceae (Hershkovitz, 1992), including species of *Calandrinia* sect. *Acaules* (Kelley & Swanson, 1985). Phylogenetic resolution within *Lewisia* will establish its primitive character states, and hence clarify its relationships to other genera, including *Calandrinia* and *Montiopsis*. Also, in the present analysis I found *Talinum* to be polyphyletic and *T.* sect. *Phemeranthus* as a possible sister group of *Rumicastrum*. The first result is consistent with Carolin's (1987). Nevertheless, both results should be regarded as highly suspect until the putative distinctions between the *Talinum* OTUs are better articulated. Also questionable is an especially close relationship between *Calyptrotheca* and *Portulacaria* + *Ceraria*. *Calyptrotheca* includes two arborescent species that otherwise resemble *Talinum* sect. *Talinum* species and differ from *Portulacaria* and *Ceraria* in having broad, not especially succulent leaves and showy flowers with numerous stamens and ovules. Figure 1 shows opposite leaves as a synapomorphy of *Calyptrotheca* with *Portulacaria* + *Ceraria*, but subopposite leaves characterize *Talinum paniculatum* (Jacq.) Gaertn. (pers. obs.).

Consistent with Carolin's (1987) findings, the present analysis does not support any existing suprageneric taxonomy of Portulacaceae (e.g., McNeill, 1974; Nyanyano, 1990; Pax & Hoffmann, 1934), including Carolin's (in press). Each of the earlier systems contains a polyphyletic taxon, variously Talineae or Calandrinieae, that comprises one-third to one-half of all Portulacaceae genera, including *Talinum* and *Calandrinia*, but usually excludes such taxa as *Calyptrotheca* and *Calandrinia* sect. *Monocosmia*. Whatever its name or precise composition, this large taxon is misinformative and should be abandoned. Other established suprageneric categories, such as the tribe Montieae (excluding *Wangerinia*; Carolin, 1987), remain defensible cladistically.

Unfortunately, the present results do not suggest an alternative comprehensive classification. Conceivably, the eastern American/African and western American groups could constitute subfamilies, but I hesitate to formalize this because of the lack of additional evidence on their precise interrelationship and because the eastern American/African group is probably paraphyletic with respect to Basellaceae, Cactaceae, and Didiereaceae (see below). Likewise, the unresolved position of Cactaceae may confound Carolin's (1987, in press; see also Gerbaulet, 1992) otherwise defensible circumscription of tribe Portulaceae. Each of the branches from the polytomous nodes in Figure 1 might be recognized as a suprageneric taxon. As I have noted, however, some of the bifurcately resolved nodes are poorly supported or disputable. By collapsing such nodes, the suprageneric taxonomy would be nearly redundant with the generic taxonomy. Even in 107-step trees, a suprageneric classification of *Talinum* is problematic. Thus, for now, I recommend listing the genera as a single linear series with established monophyletic suprageneric categories (e.g., Montieae and Portulaceae sensu Carolin) referred to only informally. Ultimately, I believe that phylogenetic evidence will warrant segregating most or all of the western American taxa into a distinct family, expanding the existing circumscriptions of Cactaceae, Basellaceae, and Didiereaceae to include their portulacaceous sister taxa, and retaining Portulacaceae only for the monophyletic residue.

### D. PHYLOGENETIC RELATIONSHIPS OF UNANALYZED MEMBERS OF THE PORTULACACEOUS ALLIANCE

I did not include Basellaceae, Didiereaceae, Cactaceae, Hectorellaceae, *Talinella*, or *Amphipetalum* in this analysis because I have not yet studied these adequately and because I do not believe that their inclusion would affect the present conclusions regarding the circumscriptions of *Calandrinia* and *Montiopsis*. I also did not consider *Xenia*, which was segregated from *Anacampseros* (Gerbaulet, 1992) while this manuscript was in review. All but Hectorellaceae probably belong to the eastern American/African clade as evidenced by their nonrosettiform habit, nonclasping, constricted leaf bases, parallelocytic/nonbrachyparacytic stomata, and (although unknown for *Amphipetalum*) copious mucilage (Cronquist, 1981; Eggli, 1984; Gibson

& Nobel, 1986; Hershkovitz, unpublished; Paliwal, 1965; Rauh, 1956; Bacigalupo in Spichiger, 1988). These taxa will be considered in future work, but a summary of existing information can be included here.

*1. Basellaceae.* Basellaceae have nearly always been linked with Portulacaceae (reviewed in Sperling, 1987), especially with *Ceraria* and *Portulacaria* because of their single-seeded indehiscent fruits (Pax & Hoffmann, 1934; Sperling, 1987). Basellaceae agree better with *Talinum* sect. *Talinum* in leaf venation pattern (Hershkovitz, unpublished), more herbaceous habit (at least the leaves and leafy stems), and panaperturate pollen (vs. tricolpate in *Ceraria* and *Portulacaria*; cf. Sperling, 1987). Unlike *Ceraria* and *Portulacaria*, Basellaceae and *Talinum* lack epidermal wax crystals (Engel & Barthlott, 1988), but this may be a symplesiomorphy. Evidence for a close Basellaceae–Didiereaceae sister group relationship (Rodman et al., 1984) is problematic (Hershkovitz, 1989). Actually, Basellaceae and Didiereaceae do share traits, e.g., single-seeded, indehiscent fruits, but in the context of Portulacaceae, these would be, at best, symplesiomorphies (i.e., with *Ceraria* and *Portulacaria*).

*2. Didiereaceae and Talinella.* Didiereaceae resemble *Ceraria* and *Portulacaria* in gross form, leaf venation pattern (Hershkovitz, unpublished), floral and inflorescence morphology (Rauh & Schölch, 1965), and epidermal micromorphology (Engel & Barthlott, 1988). Didiereaceae have also been linked with Cactaceae on the basis of serological evidence (Jensen, 1965), vegetative anatomy (Rauh, 1983; Rauh & Dittmar, 1970; Rauh & Reznik, 1961), and graft compatibility (see Cronquist, 1981; Gibson & Nobel, 1986; Rauh, 1983). Existing arguments are moot if both Cactaceae and Didiereaceae are interrelated via Portulacaceae and their similarities attributed to symplesiomorphy. Important differences between Didiereaceae and Cactaceae include perianth morphology, the absence of axillary hairs/scales in the former, and their biogeographic remoteness. Didiereaceae also resemble *Talinella* in their woody habit, much-branched inflorescences, and small flowers (Hershkovitz, 1991d; cf. Baillon, 1886; Carolin, in press; Pax & Hoffmann, 1934). The affiliation of *Talinella*, a poorly known Madagascar-endemic genus of 2–4 spp., with Portulacaceae has been questioned (Carolin, in press; Nyanyano, 1986b; Pax & Hoffman, 1934). *Talinella* is distinctive in having axile rather than free-central placentation, but its combination of betalain pigments, globular sieve-tube plastid inclusions, dichlamydous perianth, bipartite calyx, and nonbrachyparacytic or parallelocytic stomata (Behnke et al., 1975; Nyanyano, 1986b) along with normal secondary growth and copious mucilage (pers. obs.) does not occur outside of the eastern American/African group of the portulacaceous alliance. Within this group, the balance of its features suggests that *Talinella* is closest to Didiereaceae, *Ceraria*, and *Portulacaria*.

*3. Cactaceae.* A close relationship of Cactaceae to Portulacaceae has been advocated previously (Chorinsky, 1931; Gibson & Nobel, 1986; Schumann, 1899; Thorne, 1976, 1983) and perhaps indirectly via Didiereaceae (Jensen, 1965; Rauh, 1983; Rauh & Dittmar, 1970), but the position of Cactaceae among Centrospermae (indeed, among angiosperms) has been at least as controversial as Centrospermae origins and phylogeny as a whole (see, e.g., Benson, 1982; Bittrich & Hartmann, 1988; Boke, 1964; Buxbaum, 1949; Croizat, 1960; Cronquist, 1981, 1988; Engler, 1925; Erbar, 1986, 1988; Leins & Schwitalla, 1986, 1988; Leuenberger, 1986; Moeliono, 1970; Takhtajan, 1980, 1986; Zimmerman, 1985). Traits of Cactaceae that, compared to other Centrospermae, support a relationship with Portulacaceae include the combination of betalains, normal secondary growth, and petals (see Cronquist, 1981). There is general agreement that the leafy genus *Pereskia* is the most primitive among cacti, but opinions differ as to which species is the most primitive *Pereskia* (compare, e.g., Gibson & Nobel, 1986; Leuenberger, 1986). Both Leuenberger (1986) and Gibson & Nobel (1986) presumed that one or another arborescent, tropical, northern South American *Pereskia* species was primitive in the genus, although arborescence in the portulacaceous alliance is otherwise restricted to African taxa and only a few otherwise widely distributed species of Portulacaceae occur in northern South America. Leuenberger (1986) presumed that a shrubby (vs. arborescent) habit, tuberous roots, and stem stomata are derived traits within *Pereskia*, yet all occur among eastern American/African Portulacaceae (Carolin, in press; pers. obs. for stem stomata, e.g., in *Talinum* spp.).

The presence of axillary hairs and scales in Cactaceae (Chorinsky, 1931; Schumann, 1899) suggests a relationship to the clade comprising *Portulaca*, *Anacampseros*, *Talinaria*, *Talinopsis*, and *Grahamia* (Fig. 1). Among these, the poorly studied monotypic, Patagonian genus *Grahamia* resembles *Pereskia* most closely. *Grahamia* is a

woody scrambler with proleptic shoots that terminate in a single showy flower subtended by a whorl of somewhat spinescent sepaloid bracts (Carolin, in press; Pax & Hoffmann, 1934; cf. Leuenberger, 1986). A close *Grahamia–Pereskia* relationship might be counterevidenced by traits diagnosing the monophyly of Gerbaulet's (1992) "*Anacampseros* group," as well as by the chromosome base number 11 in Cactaceae versus nine in Carolin's Portulaceae. A more detailed evaluation of the evidence on cactus origins, however, is beyond the scope of the present paper.

*4. Hectorellaceae.* At present, I am unable to discern any known features of the geophytic, New Zealand endemic Hectorellaceae that would allow its unequivocal assignment to either the eastern American/African or western American groups of Portulacaceae (cf. Nyanyano, 1986a; Skipworth, 1961). Hectorellaceae are copiously mucilaginous (Yoong et al., 1975) with apparently anomocytic (Skipworth, 1961), brachyparacytic, or even cylclocytic stomata (Hershkovitz, unpublished). The leaves are highly reduced and specialized, however, so it is difficult to compare their morphology with leaves of other Portulacaceae.

*5. Amphipetalum.* Bacigalupo (in Spichiger, 1988) proposed a close relationship between *Amphipetalum* and *Calyptrotheca* because they share 6-valvate acropetally dehiscent capsules. This trait has been reported to occur in *Talinum* (*Talinum*) *rivae* Chiov. (von Poellnitz, 1934b; cf. Carolin, in press), but perhaps this Somalian endemic actually belongs to *Calyptrotheca*. Acropetally dehiscent 3-valvate capsules occur in *Talinum paniculatum* (Jacq.) Gaertn., however (Galati, 1986). The herbaceous habit, small size (< 0.5 m high), sparsely or unbranched inflorescence, numerous ovules (> 10), and ≥ 40-porate pollen of *Amphipetalum* are contrary to the traits of *Calyptrotheca* and suggest a closer relationship to *Talinum* section *Talinum* spp. (Carolin, 1987, in press; Nyanyano, 1986a; Pax & Hoffmann, 1934), although the pollen pore number of *Amphipetalum* exceeds that reported in any species of *Talinum*. *Amphipetalum* shares with *Montiopsis* an indumentum of uniseriate, multicellular trichomes.

### E. WHAT IS PRIMITIVE IN THE PORTULACACEOUS ALLIANCE?

The consensus tree (Fig. 1) is disappointing in its failure to identify which taxon or taxa form the sister group of the remainder. Table 4 shows that several resolutions are possible among the 107-step trees, and many more emerge when an additional step is allowed. But this result is possibly as informative as it is uninformative, i.e., it shows that the distributions of putatively primitive traits in the family are poorly correlated. For example, tricolpate pollen does not co-occur with the chromosome base number nine (Appendix 1; cf. Table 3). The paradoxical discordance of character state distributions can be appreciated in view of the following speculative model of portulacaceous evolution based on biogeography.

Biogeographic evidence might suggest that the eastern American/African group is more ancient than the western American. The former group, with or without *Rumicastrum*, is distributed in three Gondwanan continents and Madagascar. Basellaceae (aside from cultivated and/or weedy species; see Sperling, 1987), Cactaceae, *Talinum*, *Anacampseros/Talinaria*, *Portulaca*, and possibly *Amphipetalum/Calyptrotheca* are disjunct between America and Africa. *Portulaca* and *Anacampseros* are also disjunct to Australia (Carolin, 1987; Geesink, 1969; Pax & Hoffmann, 1934). Except for the African species of *Rhipsalis*, the disjunct taxa do not appear to be specialized for long-distance dispersal, which suggests that the eastern American/African group may have differentiated during a period when the flora was more easily interchanged, i.e., ca. 50 million years ago or earlier (cf. Gibson & Nobel, 1986; Leroy, 1978; Raven, 1983; Raven & Axelrod, 1974). Endemism in the western American group is almost entirely limited to generally montane and/or desert regions of temperate western America. The exceptions include a distinctive species of *Montia* in Australia/New Zealand (Nilsson, 1966a) and other eastern American or Eurasian species of Montieae that are otherwise closely related to western American species (cf. McNeill, 1975). That *Calandrinia* (*Calandrinia*) *ciliata* is native to Australia (cf. von Poellnitz, 1934a) has not been confirmed (Kelley, 1973; cf. West, 1986). Considering that the geophysical events responsible for creating the present-day ecological attributes of temperate western America are believed to have occurred within the last 15 million years, one might conclude that the western American group differentiated much more recently than the eastern American/African group (cf. Raven & Axelrod, 1978; Solbrig, 1976). Moreover, the North American taxa of this group are believed to have been derived from the South American (Raven & Axelrod, 1978; but see also Hershkovitz, 1991a).

Contrary to the biogeographic scenario, the cladistic results suggest that the western American

group is as old as if not older than the eastern American/African group (Fig. 1). The positions of individual taxa in the consensus tree are sometimes no less counterintuitive. For example, *Portulaca* might seem to be relatively primitive among Portulacaceae: It occurs on three southern continents, most species have the typical centrospermous chromosome base number nine, and some species have the putatively primitive inflorescence type for the family (Carolin, 1987; Geesink, 1969, 1987). *Portulaca* is epigynous and has $C_4$ photosynthesis, but these are likely autapomorphies. Yet, in Figure 1, *Portulaca* emerges as derived among Portulacaceae because of its panaperturate pollen and axillary hairs and scales. The only tricolpate members of the eastern American/African group are *Ceraria* and *Portulacaria*, which otherwise appear derived in their growth form and fruit morphology. Many western American taxa have tricolpate pollen and, among these, species of *Lewisia* have dichasial inflorescences. Indeed, the present analysis showed *Lewisia* as a possible outgroup of the remainder of the analyzed taxa. Yet, *Lewisia* is characterized by a derived fruit type, and the species with dichasia have such derived traits as glandular-dentate sepals, laterocytic stomata, and chromosome base numbers of 12, 14, 15 (i.e., the dichasial species may be derived within *Lewisia*; Hershkovitz, 1992; cf. Mathew, 1989). Moreover, the genus is restricted to western North America.

From the above comparison, it is clear that Portulacaceae exhibit a high degree of what Takhtajan (1991 and citations therein) calls heterobathmy, i.e., a disharmonious distribution of primitive and derived traits. Takhtajan's observation that high degrees of heterobathmy characterize grade groups is perhaps applicable here in view of the probable paraphyly of Portulacaceae. Alternatively, the perception of high heterobathmy may reflect conceptual constraints as to which traits are necessarily primitive. For example, if enough phylogenetic evidence accumulates that the chromosome base number nine and perhaps even tricolpy are advanced conditions in various Portulacaceae, the degree of perceived heterobathmy in the group would be reduced.

### F. THE PORTULACACEOUS ALLIANCE AND CENTROSPERMAE PHYLOGENETIC RESOLUTION

The results of the present analysis accord with my earlier admonition that progress in resolving Centrospermae phylogeny is constrained by poor understanding of phylogeny within the included traditional families (Hershkovitz, 1989, 1991f). Higher-level phylogenetic analysis requires comparison of demonstrably or at least plausibly primitive character states of polymorphic taxa. For Portulacaceae, a set of putatively primitive character states cannot at present be established because different polarities for several characters remain equally defensible. Moreover, the results presented here indicate that some traits present among Portulacaceae and typical of possible centrospermous outgroups, such as the chromosome base number nine, cannot be presumed primitive in the former. Finally, the likelihood that other traditional centrospermous families, i.e., Cactaceae, Basellaceae, Didiereaceae, and Hectorellaceae, are phylogenetically nested within Portulacaceae suggests that phylogenetic analysis among the last must precede advances in the understanding of the first three.

The hindsight provided by formal cladistic analysis is not required to appreciate these precautions. Irrespective of the taxonomic system followed, even the most rudimentary analysis of character variation among Portulacaceae should reveal the extent of polymorphism at lower taxonomic levels and indicate that the primitive character states for the family are not readily discernable. Likewise, close relationships of Cactaceae, Basellaceae, Didiereaceae, and Hectorellaceae to specific members of Portulacaceae rather than to the family as a whole were explicitly proposed in classical literature. The portulacaceous alliance is not unique in its degree of phylogenetic irresolution and possible paraphyly of familial and lower level taxa: similar taxonomic problems characterize other Centrospermae as well (Hershkovitz, 1991e, f).

This emphasis on problems of polymorphism and paraphyly should not imply that portulacaceous and/or Centrospermae phylogeny are hopelessly complex and unresolvable. Rather, inroads are possible by preliminary resolution of such problems at the lower taxonomic levels, such as that presented here for *Calandrinia* sensu lato. Additional progress in resolving portulacaceous phylogeny will be facilitated by similar analysis of other polymorphic taxa, e.g., *Talinum* and *Lewisia*. Collectively, such studies will help consolidate the portulacaceous OTUs, thereby facilitating analysis of Centrospermae as a whole. Naturally, scrutiny of lower level taxa in other Centrospermae will also be required.

## CONCLUSIONS

Although phylogeny of Portulacaceae remains poorly resolved, the present cladistic analysis supports the segregation of *Montiopsis*, *Cistanthe*,

*Rumicastrum*, and *Schreiteria* from *Calandrinia*. *Calandrinia* should be restricted to sections *Calandrinia*, *Monocosmia*, and *Acaules*. The first two may be cladistically nested in the last, and section *Monocosmia* may be nested in section *Calandrinia*. *Montiopsis* is a monophyletic genus with two subgenera, *Montiopsis* and *Dianthoideae*, and the latter may be paraphyletic. *Calandrinia* and *Montiopsis* are possibly sister groups but uncertainty to this effect and the distinctions between the two genera warrant their separation. The present analysis also supports my earlier circumscription of *Cistanthe* (Hershkovitz, 1991a) and hypothesized distinction between the eastern American/African and western American members of Portulacaceae. Otherwise, relationships among Portulacaceae and members of this family to Basellaceae, Cactaceae, Didiereaceae, and Hectorellaceae remain poorly resolved. The number and magnitude of unresolved problems preempt, for now, the reliability of familial-level phylogenetic analyses of Centrospermae (cf. Rodman, 1990). Some of the problems are, at present, more approachable than others, and subsequent research should emphasize analyses of the more polymorphic genera.

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APPENDIX 1. Characters and character states for Portulacaceae. Listed below are the characters, analyses, and states used in the present cladistic analysis. The scores for the taxa are provided in Table 3. Where presumed, effective polarities, i.e., characters scored as "0" in the hypothetical ancestor, are indicated. The "0" designation also denotes a posteriori determined primitive states. Otherwise, the state designations are arbitrary.

HABIT (CHARS. 1–3)

Portulacaceae are sorted here according to their woodiness, presence of a basal leaf rosette, and phenology. Other Centrospermae are variously woody or herbaceous; therefore, the polarity of this character is equivocal, although, unlike members of the portulacaceous alliance, most other woody Centrospermae have anomalous secondary thickening (Cronquist, 1981). Portulacaceae can be largely sorted according to those that produce a prominent basal or suprabasal rosette in which axillary, ephemeral aerial flowering stems arise versus those in which the aerial stems proliferate vegetatively. Even these two categories intergrade, e.g., in *Montiopsis*. Studies of seedling development may permit better assignment of character states and/or evaluation of the validity of this character. Both growth forms occur commonly in other Centrospermae, hence I designate no polarity. I presume perennials persisting via the caudex or main stem to be primitive with respect to annuals. I scored *Naiocrene* as perennial and *Montia* as annual. Perennials occur among the latter, but they apparently persist via stolons rather than a caudex or main crown (Nilsson, 1966a).

Carolin (1987) and Gerbaulet (1992) employed alternative character state definitions in their analyses. Carolin (1987) categorized Portulacaceae variously as phanerophytes, passive chamaephytes, active chamaephytes (including protohemicryptophytes and rosette hemicryptophytes), and therophytes. For Portulacaceae, the first three categories intergrade, i.e., some taxa scored by Carolin as passive chamaephytes (e.g., *Talinum* sect. *Talinum*) perennate via distal buds on erect branches rather than from rosette axils (e.g., in *Cistanthe* spp.). The former condition seems more akin to the phanerophytic habit, and the latter to rosette hemicryptophytes. *Calandrinia* sect. *Acaules* and most *Lewisia* spp. must be regarded as rosette hemicryptophytes, rather than passive chamaephytes as Carolin scored them. The active chamaephyte category is ignored here because so characterized Portulacaceae seem to be derived members of otherwise rosette-forming perennial taxa, e.g., *Claytonia* species. Gerbaulet (1992) recognized three size classes of chamaephytes and four types of habit (including rosettiform). Her data indicate that my scoring of *Anacamsperos* sect. *Tuberosae* as rosettiform is incorrect.

1. Stems herbaceous or woody only at the base, 0; stems becoming woody throughout, 1.
2. Plants not rosettiform, 0; plants rosettiform, 1.
3. Plants perennial, 0; plants annual, 1.

ROOTS (CHAR. 4)

Carolin's (1987) characters and scoring are adopted here. Tuberous roots are uncommon outside of the portulacaceous alliance, and I presume them to be derived. Syeda & Ashton (1989) presumed tuberous roots to be a derived trait for *Rumicastrum*, but tuberous roots occur in the perennial species (Pate & Dixon, 1982), so I scored *Rumicastrum* as tuberous.

4. Roots not tuber-forming, 0; roots tuber-forming, 1.

STEMS (CHARS. 5, 7)

Carolin's (1987) interpretation and scoring are adopted here. Unless axillary hairs and scales/bristles are considered homologous to stipules in Caryophyllaceae and/or Molluginaceae, these structures are presumably derived. Gerbaulet (1992) recognized several scale types within *Anacampseros*, and she scored scale morphology in *Grahamia*, *Talinaria*, and *Talinopsis* as unknown. Her results also indicate that, contrary to my score, axillary hairs are primitively absent in *Anacampseros* sect. *Avonia*.

5. Stems without axillary hairs, 0; stems with axillary hairs, 1.
6. Stems without axillary scales/bristles, 0; stems with axillary scales/bristles, 1.

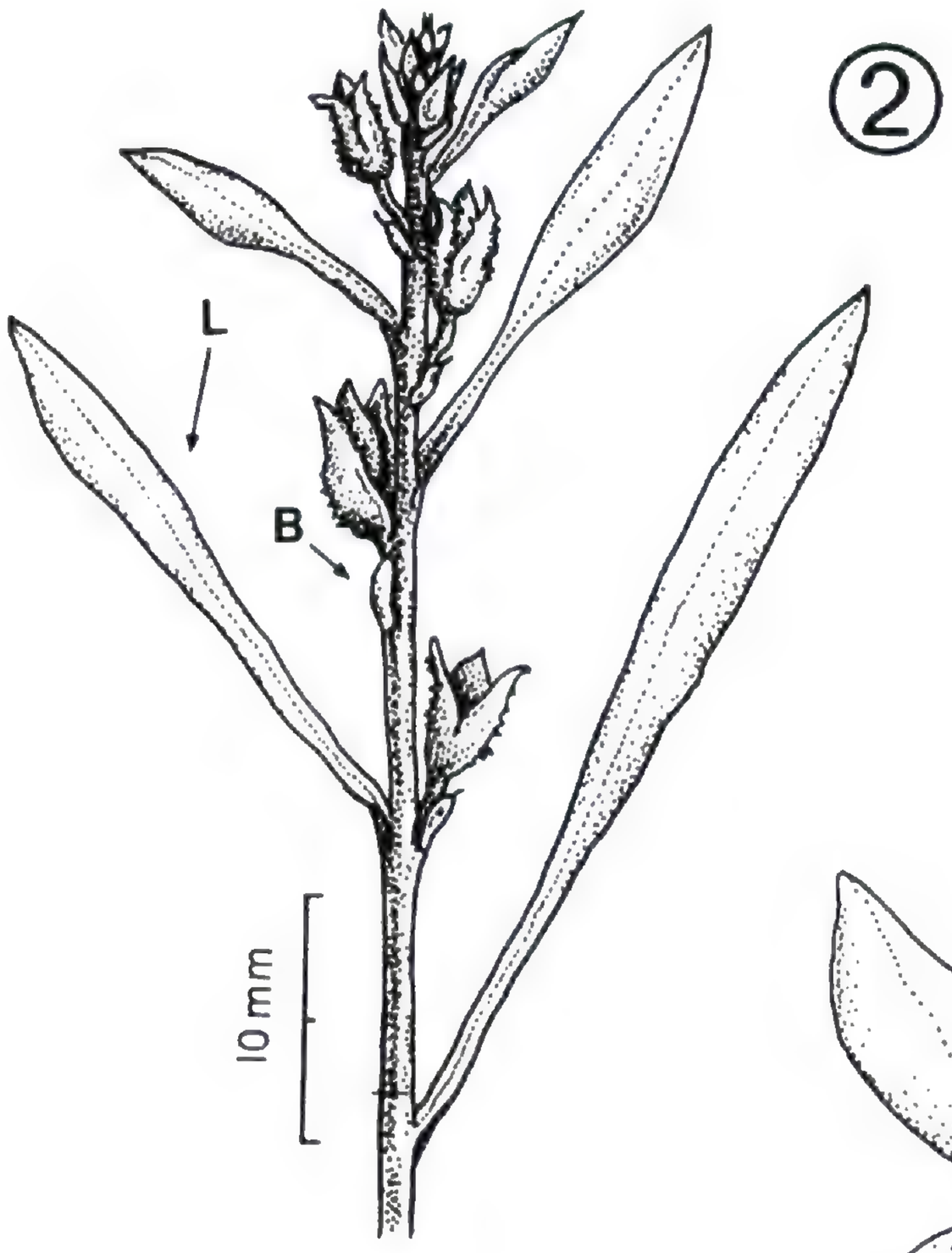
LEAVES (CHARS. 7–21)

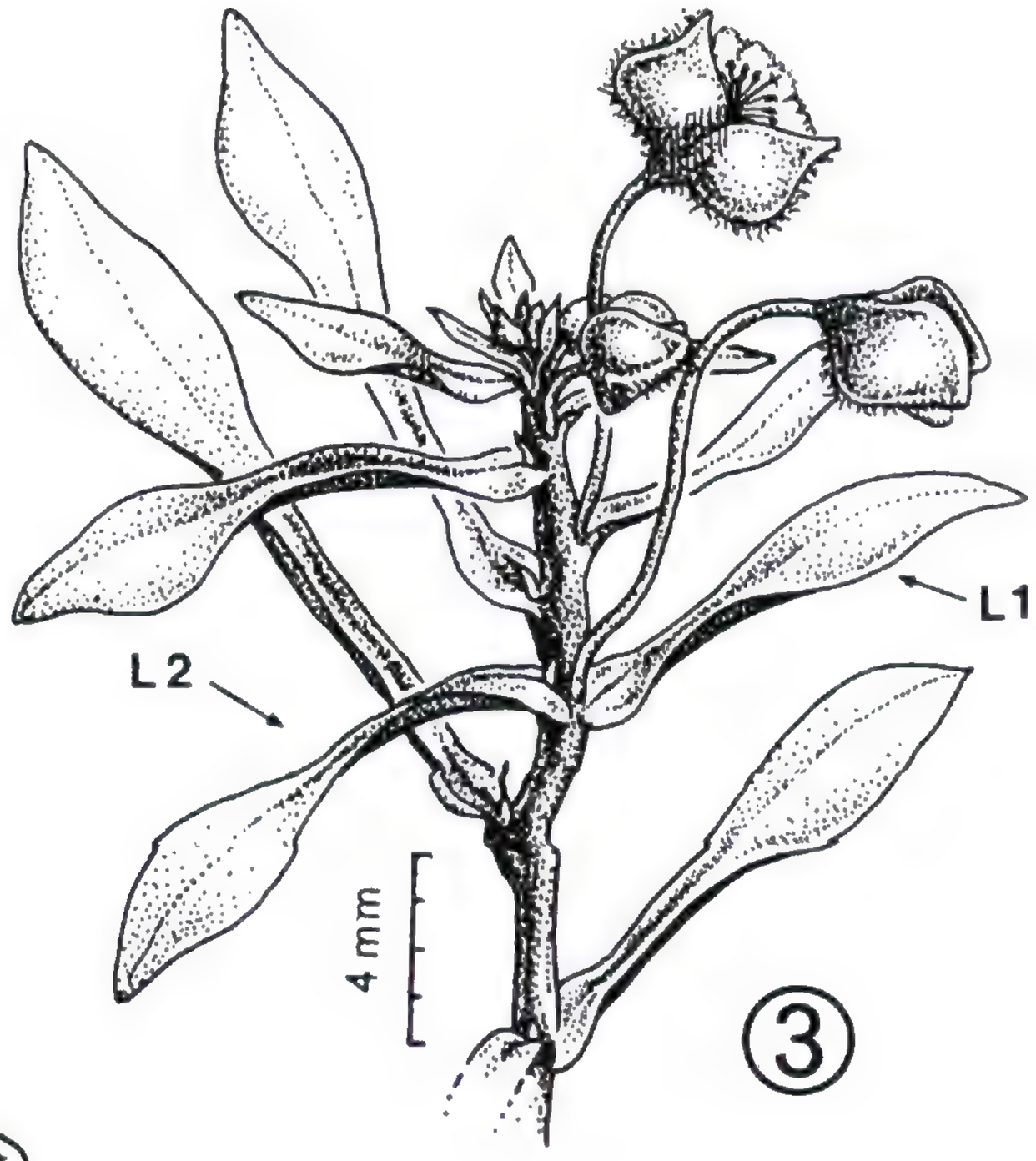
The leaf characters and data are from Hershkovitz (1990a, 1991b, 1992, 1993, unpublished), including reevaluated data from Becker (1895), Carolin (1987), Kelley (1973), Metcalfe & Chalk (1950), Nilsson (1966a, 1970, 1971a, b), and references cited in these. I exclude several characters that I have reported on elsewhere because of excessive infra-OTU variation, lack of variation at the level of the present OTUs, and/or inadequate data. These include petiole morphology, primary vein anatomy, vein density, presence of three-dimensional venation, the number of epidermal cells in contact with the guard-cell pair, the presence of an outer cycle of subsidiary-like cells (Hershkovitz, 1993), stomatal density, and stomatal index.

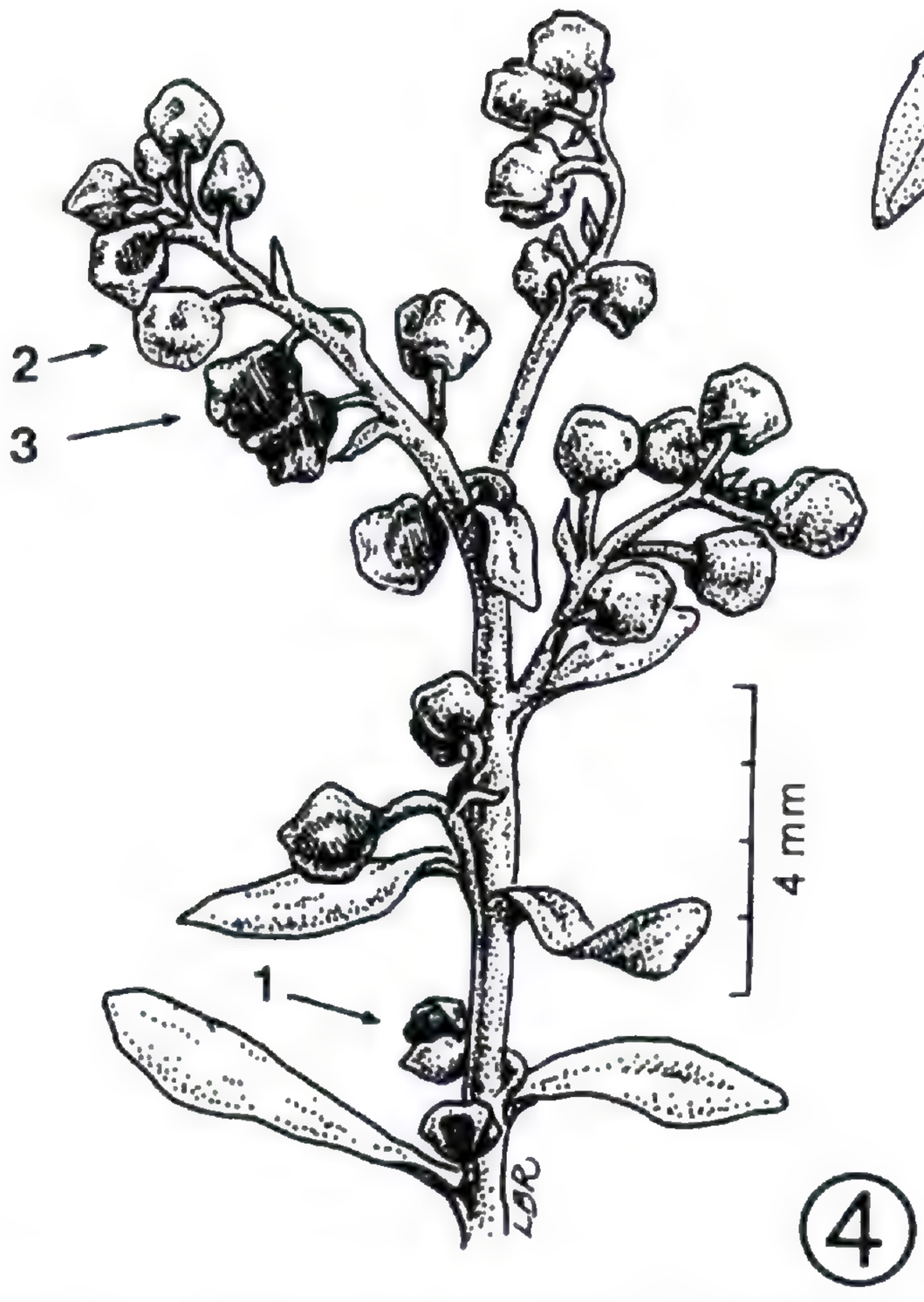
*A. Leaf position.* I tentatively presume alternate leaves to be primitive, but opposite leaves occur in many Caryophyllaceae, Molluginaceae, and Aizoaceae. Carolin misscored this character for *Calyptrotheca*. Opposite leaves are rare in *Portulaca* but characterize the putatively most primitive species (Geesink, 1969, 1987). I scored the genus as "?".

7. Leaves alternate, 0; leaves opposite, 1.

*B. Leaf base morphology.* Clasping, nonclasping, jointed, and nonjointed leaf bases occur in other Centrospermae, hence I designate no polarity for the leaf base characters. I previously interpreted the leaf bases of *Rumicastrum* as clasping (Hershkovitz, 1990a), but according to West (1986), they are not. My interpretation was based on herbarium, rather than live specimens, so I here




FIGURES 2–4. Inflorescence morphology in *Calandrinia*. — 2. Inflorescence of *Calandrinia* (*Calandrinia*) *ciliata* [U.S.A., California: *Hershkovitz s.n.* (spirit collection)]. Note the lack of dense coiling and the leaf (L) and bract (B) associated with each flower. — 3. Inflorescence of *Calandrinia* (*Calandrinia*) *axilliflora* [Chile, Region O'Higgins:

adopt West's opinion. It is possible that *Rumicastrum* is intermediate for this character.

8. Leaf bases jointed, 0; leaf bases not jointed, 1.
9. Leaf bases clasping, 0; leaf bases not clasping, 1.

*C. Leaf mucilage cells.* Copious mucilage production by relatively large numbers of foliar mucilage cells does not appear to be common among other Centrospermae; hence I presume it to be derived. Copious mucilage production characterizes at least some species of *Cistanthe* and *Rumicastrum,* but I have not adequately surveyed either genus; hence I scored these as unknown. Mucilage cells occur in *Calandrinia* sect. *Calandrinia* and species of *Lewisia* (Becker, 1895), but the mucilage content of the leaves appears to be relatively slight (pers. obs.).

10. Leaf mucilage cells none or few and not conspicuous, 0; leaf mucilage cells conspicuous and relatively numerous, 1.

*D. Leaf vein anatomy.* I have not found ribbonlike veins (Hershkovitz, 1991b) to occur among other Centrospermae; hence I presume them to be derived. This character proved difficult to score: minor veins in leaves of some taxa are almost always ribbonlike, but in other taxa they are only weakly manifested. There may be no distinct boundary between the character states, and ribbonlike veins may prove to be at least infrequently present in taxa scored as absent. The scoring adopted here for variable taxa biases against homoplasy.

11. Ribbonlike veins absent, 0; ribbonlike veins present, 1.

*E. Leaf venation pattern.* Festooned brochidromous venation occurs among other Centrospermae, although simple brochidodromous is more common. Without more confidence as to which Centrospermae are closest to the portulacaceous alliance, I leave the polarity uncertain. Festooned brochidodromy intergrades with simple brochidodromy among Portulacaceae and, among the OTUs scored as present, is absent in the smallest and/or narrowest leaves. The scoring adopted here for variable taxa biases against homoplasy.

12. Leaf venation not festooned brochidodromous, 0; leaf venation festooned brochidodromous, 1.

*F. Leaf fimbrial vein.* Fimbrial veins occur in other Centrospermae but only in otherwise apparently derived taxa (e.g., among Caryophyllaceae subfamilies Alsinoideae and Caryophylloideae). Thus, I presume fimbrial veins to be derived in Portulacaceae. There are two types of fimbrial veins in Portulacaceae: those that become perpendicular to the primary vein at the leaf apex, and those that become more parallel (Hershkovitz, 1990a, 1993). The transformation series adopted here permits fimbrial vein presence to serve as a synapomorphy while requiring only one step between each of the three states. I scored *Calandrinia affinis* as present for fimbrial veins, although the species is variable for the trait, and I am not certain that my specimens are correctly determined (cf. Hershkovitz, 1993).

13. Fimbrial vein absent, 0; fimbrial vein present, 1.
14. Fimbrial vein becoming perpendicular to the primary vein at the apex, 0; fimbrial vein parallel to the primary vein at the apex, 1; fimbrial vein absent, X.

*G. Stomata.* Parallelo- and/or nonbrachyparacytic stomata (see Hershkovitz, 1990a, 1991b) do not appear to be common outside of the portulacaceous alliance; hence I am inclined to presume that this state is derived. The most common stomatal type outside of the alliance, anomocytic (Hershkovitz, unpublished; Metcalfe & Chalk, 1950), is rare and probably derived within the alliance. Hence I leave the stomatal type polarity undetermined. Brachytetra- and staurocytic stomata are presumably derived with respect to brachyparacytic. I presume that laterocytic stomata, which are apparently restricted to *Lewisia* spp., are derived from brachyparacytic (Hershkovitz, 1992). Likewise, I presume that anomocytic stomata of *Montia* spp., *Lewisia* spp., and *Montiopsis* spp. (Hershkovitz, 1990a, 1992, 1993; Metcalfe & Chalk, 1950; Nilsson, 1966a, 1970, 1971a, b; Nyanyano, 1986a, c) are derived from brachyparacytic, which characterize other species of these genera. Brachytetra-/staurocytic stomata occur in *Montiopsis* sect. *Dianthoideae*, but I scored this taxon for their absence.

15. Stomata predominantly brachyparacytic and/or similar types (see Hershkovitz, 1990a, 1991b), 0; stomata predominantly parallelocytic and/or nonbrachyparacytic, 1.
16. Stomata predominantly brachyparacytic, nonbrachyparacytic, or parallelocytic, 0; stomata commonly brachytetracytic and/or staurocytic, 1.

*H. Foliar trichomes.* Several trichome types have a limited distribution among Portulacaceae. Trichomes occur commonly among Centrospermae; hence no polarities are presumed within Portulacaceae. I have adopted a transformation series that treats unicellular trichomes as an intermediate in deriving ribbed, glandular, multicellular and/or multiseriate trichomes (see Kelley, 1973). Unicellular foliar trichomes occur in several eastern American/African OTUs, although Carolin (1987) scored all of these as lacking such. I scored OTUs possessing trichomes as present unless I believed them to be unquestionably derived therein. Gerbaulet's (1992) results indicate that I should have scored *Talinaria* and possibly *Ceraria* as possessing trichomes, and *Anacampseros* sect.

←

*Gay s.n.* (P)]. Note the lack of dense coiling and the two leaves (L1 and L2) associated with each flower.—4. Terminal branch of highly ramified inflorescence of *Calandrinia* (*Monocosmia*) *monandra* [Argentina, Río Negro: *Buchtien 37* (US)]. Some flowers are solitary and axillary (1), some are associated with bracts (2), and some are apparently bractless (3). Drawings by Leslie Randall.

FIGURE 5. Cleared developing inflorescence of *Claytonia sibrica* L. [U.S.A., California: near Hupa, *Manning s.n.* (UC)] showing dense coiling. Scale bar = ca. 3 mm.

*Tuberosae* should have been scored as lacking them. Trichomes do not occur in *Montia* (contra Carolin, 1987, appendix 2), and if unicellular trichomes in *Calandrinia* sect. *Acaules* spp. are indeed glandular, they are probably not homologous to multicellular glandular trichomes of *Montiopsis* (cf. Carolin, 1987). I have not been able to confirm the presence of trichomes in *Lenzia* (cf. Carolin, 1987). Unribbed unicellular trichomes have been reported in *Rumicastrum quadrivalvis* F. Muell., ined. (Kelley, 1973), but I have been unable to verify the identity of the examined specimen (Hershkovitz, 1993). In any case, I scored *Rumicastrum* as absent. Epidermal papillae occur in several other Portulacaceae, including *Montia* and *Cistanthe* (Hershkovitz, 1990a, 1991b). Here, I distinguish between papillae, which are merely swollen epidermal cells, and trichomes, in which the center of the emergent cell wall has a distinct U- or V-shaped protuberance. Gerbaulet (1992) used the term "papillae" for what I here consider trichomes. Finally, I have adopted "X" scoring for the ribbed trichome character so that the interderivation of ribbed, unribbed, and no trichomes requires a single step.

17. Foliar trichomes absent, 0; foliar trichomes present, 1.
18. Foliar trichomes unicellular, 0; foliar trichomes multicellular, 1.
19. Foliar trichomes uniseriate, 0; foliar trichomes multiseriate, 1.
20. Foliar trichomes nonglandular, 0; foliar trichomes glandular, 1.
21. Foliar trichomes nonribbed, 0; foliar trichomes ribbed, 1; foliar trichomes absent, X.

INFLORESCENCE (CHARS. 22–26)

*A. Inflorescence type.* I tentatively concur with Carolin (1987) in presuming that monochasia and solitary flowers are derived in Portulacaceae. That metaxytriads are primitive cannot be established a priori, however (cf. Carolin, 1987): this type was unequivocally derived in Carolin's cladogram.

Carolin (1987) interpreted the inflorescence in *C.* sect. *Calandrinia* as monochasial, but I regard the "inflorescence" to be a vegetative sympodium with solitary, axillary flowers. In the context of Weberling's (1989) definition of an inflorescence, my interpretation is problematic but, nevertheless, emphasizes the evident distinction in inflorescence morphology between section *Calandrinia* and Portulacaceae with unquestionably monochasial inflorescences. In *Cistanthe* and Montieae, for example, including *Claytonia sibirica* L. (Fig. 5), the developing inflorescence is strongly coiled, and the inflorescence bracts are much smaller than foliage leaves or, in some species, absent. In *Calandrinia* (*Calandrinia*) *ciliata* (Ruiz & Pavón) DC. (Fig. 2), the developing inflorescence is cincinnoid but leafy throughout. Each flower is associated with one leaf and one small bract, and the cauline leaves are gradually reduced distally but otherwise identical to the basal leaves. Axillary buds occur in both the leaf and bract axils (pers. obs.). In *Calandrinia axilliflora* Barnéoud (Fig. 3), flowers arise from the axils of otherwise normal foliage leaves that alternate with leaves having vegetative axillary buds. In some specimens, the inflorescence has very short internodes and thus resembles a whole rosettiform plant of *Calandrinia* sect. *Acaules*. The character scoring I adopt for section *Calandrinia* is obviously interpretation-laden; hence the results must be judged accordingly. *Calandrinia* (*Monocosmia*) *monandra* (Ruiz & Pavón) DC. (Fig. 4) has a unique inflorescence structure that I cannot classify. It is highly branched, the main stem is leafy toward the base, and both single flowers and multiflowered branches may arise from leafy, bracteate, or naked nodes. I have also observed cauliflory in this species. Since my earlier work (Hershkovitz, 1990a), I have also reexamined the inflorescence of *Montiopsis* and have concluded that it conforms to either a botryoid or a bostryx (cf. Weberling, 1989)—either way, the inflorescence is similar in all members of the genus and distinct from other Portulacaceae (cf. Carolin, 1987). My new interpretation is based only on studies of herbarium material and requires developmental analysis to verify.

I tentatively scored *Lewisia* for having dichasia, but monochasia and solitary flowers also occur in this genus (Hershkovitz, 1992; Mathew, 1989). It is possible that dichasia are secondary in *Lewisia* because they occur in species with a presumably derived chromosome base num-

ber (Hershkovitz, 1992). Solitary flowers also occur in *Anacampseros* sect. *Avonia*, *Talinum* sects. *Talinum* and *Phemeranthus*, and *Rumicastrum* (von Poellnitz, 1933, 1934a, b), but I presume that this is not the primitive condition. In any case, the transformation series I adopt here requires only one step between dichasia, cincinni, botryoids/bostryces, and solitary flowers, while metaxytriads are scored as one step from dichasia and two steps from the other types, assuming that dichasia would constitute an intermediate state.

22. Flowers in metaxytriads, 0; flowers not in metaxytriads, 1.
23. Flowers in metaxytriads or dichasia, 0; flowers in nonleafy cincinni, 1; flowers in botryoids/bostryces, 2; flowers solitary or apparently in cincinni with at least one normal foliage leaf per flower, X.
24. Flowers not solitary, 0; flowers solitary or apparently in cincinni with at least one normal foliage leaf per flower, 1.

*B. Inflorescence bracts.* For inflorescence bract polarities, I concur with Carolin (1987) that two equal bracts are primitive, and that equal or subequal bracts are primitive with respect to markedly unequal. The bract size differential is also problematic. I have scored only the *Cistanthe* sections for unequal bracts, but the degree of intergradation with subequal bracts in other taxa (e.g., *Montiopsis*) should be scrutinized quantitatively. While this manuscript was in review, I reevaluated bract morphology in *Calandrinia* (see also Hershkovitz, 1993). *Calandrinia acaulis* and *C. carolinii* have jointed peduncles, with a pair of foliaceous bracts subtending the pedicel. *Calandrinia affinis* has unjointed peduncles, usually with a pair of small, scalelike bracts near the base. Rarely, one of these is foliaceous and more proximal to the flower. (Peralta (1988, fig. 2B) illustrated three bracts in *C. affinis*, two basal and scalelike and one foliaceous, but I have not observed this condition.) Based on preliminary observations, I had scored *C. affinis* as having one bract or none. Moreover, I now question my interpretation of the bracts in section *Calandrinia*. I had scored these taxa for one bract or none, but it is possible that the leaf pair in *C. axilliflora* or the leaf/bract pair in other species are homologous with the foliaceous bract pair in *C. acaulis* and *C. carolinii*. I leave this problem unresolved pending additional analysis.

25. Inflorescence bracts two per flowering node, 0; inflorescence bracts one or none, 1.
26. Bracts of a pair ± equal, 0; bracts of a pair markedly unequal, 1; bracts one or none, X.

### Perianth (chars. 27–29)

The apparently biseriate perianth of Portulacaceae has been variously interpreted as homologous to a bimerous involucre plus tepals (Cronquist, 1981, 1988; Eckardt, 1976; Gerbaulet, 1992; Stebbins, 1974) or as a true biseriate perianth (Carolin, 1987; Geesink, 1969, 1971; Milby, 1980; Sharma, 1954; Soetiarto & Ball, 1969). For practical purposes, I adopt the latter interpretation.

*A. Sepal morphology.* The degree of sepal persistence through fruit maturity varies within the taxa circumscribed here (e.g., in *Rumicastrum* spp., Syeda & Ashton, 1989; in *Talinum* spp., Macbride, 1937), but early deciduous sepals are probably primitive in some taxa. Like Carolin (1987), I scored *Talinum* for deciduous sepals, but those of *T. paraguayensis* Speg. seem perfectly persistent (pers. obs.). That persistent sepals are primitive overall is assumed, but deciduous sepals occur among other Centrospermae.

Glandular-toothed bracts and sepals occur in *Lewisia* and *Schreiteria*, and I presume them to be derived. Glandular and dentate sepals that occur in *Montiopsis* are problematic. The glands are associated with trichomes, hence I do not consider them homologous to glandular teeth. The denticulations in this genus appear to be associated with the base and flanks of the sepals and bracts, whereas those of *Lewisia* and *Schreiteria* are concentrated toward the apex. Thus, I scored *Montiopsis* as absent for glandular-dentate bracts and sepals. Some species of *Montiopsis* sect. *Montiopsis* do have lobed (dentate?) sepals, however (Ford, 1992; Peralta, 1988, figs. 6I, 7G). I interpret the sepals of some *Cistanthe* taxa, especially those of section *Calyptridium*, as erose rather than dentate. I suspect that dentate bracts in most *Lewisia* spp. are derived, but I scored the genus as present to test the remote possibility that *Lewisia* and *Schreiteria* are somehow related.

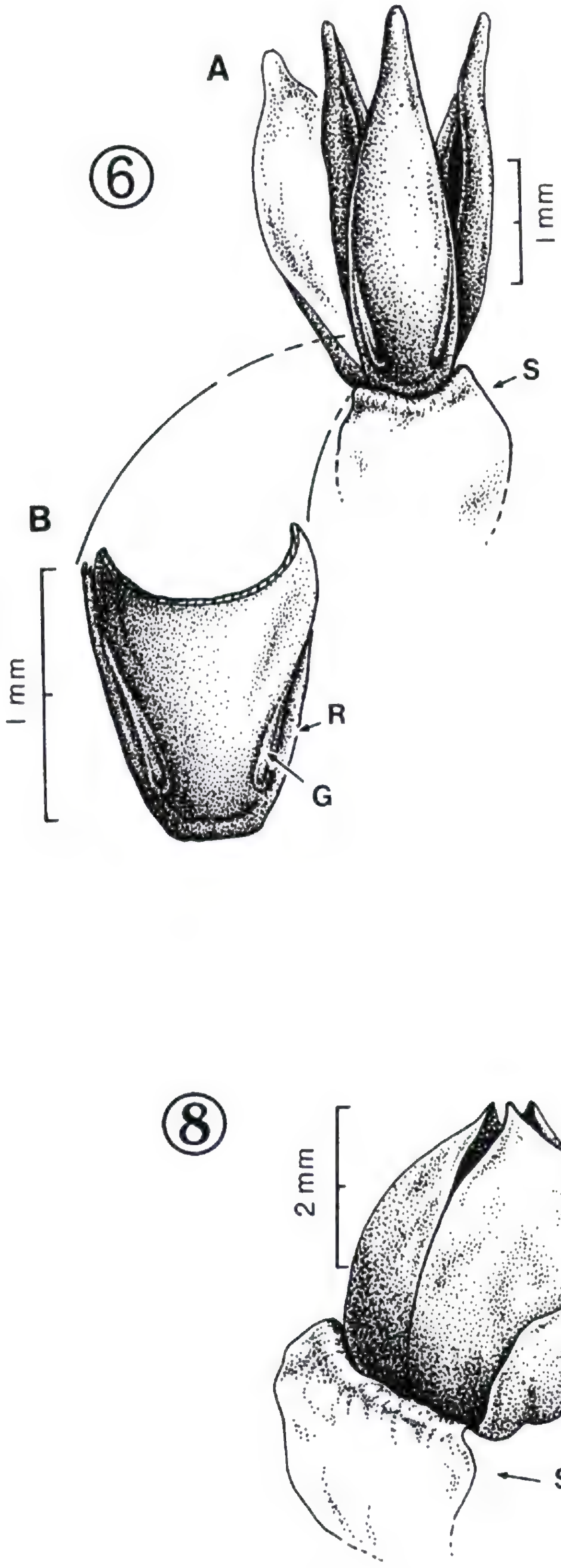
27. Sepals persistent, 0; sepals deciduous, 1.
28. Sepals and bracts not glandular-dentate, 0; sepals and bracts glandular-dentate, 1.

*B. Petal numbers.* Petal numbers are problematic because they vary within and intergrade among taxa. Some taxa, however, seem to have consistently higher petal numbers than others. Carolin (1987) presumed that higher petal numbers were primitive in Portulacaceae (as did Syeda & Aston, 1989, and Syeda & Carolin, 1990, for *Rumicastrum*), but I scored fewer petals as primitive because higher petal (or tepal) numbers are, among Centrospermae, not common outside of the portulacaceous alliance, and then they are probably independently derived (e.g., among Aizoaceae; Bittrich & Struck, 1989). Irrespective of Carolin's (1987) polarity determination for this trait, his scores for this character are sometimes incorrect; e.g., for *Anacampseros* and *Talinaria* (Pax & Hoffmann, 1934; McNeill, 1977; von Poellnitz, 1933). As with the preceding character, the score for the variable taxon *Lewisia* is experimental.

29. Petals typically five to six or fewer, 0; petals typically more than five, 1.

### Stamens

Carolin (1987) scored *Grahamia* and *Portulaca* for having connate stamens adnate to the petals. The condition in these species is possibly extreme, but similarly fused stamens are probably the general condition among Portulacaceae (see, e.g., Peralta, 1988, for *Calandrinia* sensu lato and Mathew, 1989, for *Lewisia*). I prefer not




FIGURES 6–8. Capsule morphology in *Montia* and *Calandrinia*.—6. Dehisced capsule of *Montia parvifolia* [U.S.A., California: *Thomas 3543* (US)]. A. Whole fruit showing capsule-valve inrolling, the narrow teardrop-shaped grooves near the margins of the capsule valve base, and the marginal ribs. A sepal has been folded down to show

to recognize stamen fusion as a character in this analysis. I agree with Carolin (1987) that stamen number is too highly variable within OTUs (sometimes within individuals) to be useful at the present level of analysis, especially because the outgroup condition is equivocal.

POLLEN (CHARS. 30, 31)

The pollen character transformation series proposed by Carolin (1987) is problematic because, irrespective of whether narrow- and broad-pantocolpate pollen can always be distinguished, Carolin's transformation series requires two steps between these states. Possibly intermediate states occur: several taxa reported by Carolin (1987) to be pantocolpate were reported by Nyanyano (1985, 1986a) to be pantoporate. Gerbaulet (1992) reported, however, that contrary to mine and Carolin's scores, *Anacampseros* sect. *Anacampseros* has pantoporate pollen. The transformation series adopted here presumes only that three apertures are primitive with respect to several, and that colpi are primitive with respect to pores.

30. Pollen tricolpate, 0; pollen panaperturate, 1.
31. Pollen colpate, 0; pollen porate, 1.

STIGMAS (CHARS. 32, 33)

The comments for petal number are applicable here: stigma numbers intergrade, the polarity is uncertain, and some of Carolin's (1987) scores are not in agreement with the literature, e.g., for *Anacampseros* (cf. Pax & Hoffmann, 1934; von Poellnitz, 1933). Two stigmas are unusual among Portulacaceae, however, and are presumed to be derived. The score for *Lewisia* tests the possibility that the genus is related to *Portulaca* or *Grahamia*.

32 Stigmas two or three, atypically four, 0; stigmas typically four or more, 1.
33. Stigmas three or more, 0; stigmas two, 1.

FRUIT (CHARS. 34–42)

The fruit characters, polarities, and scores proposed by Carolin (1987) are largely adopted here, with some exceptions. The polarities of the fruit epidermal cell characters are left uncertain. These characters should be better scrutinized because I believe they may intergrade more than Carolin's scoring would indicate, especially in *Talinum* sects. *Talinum* and *Phemeranthus*. The fruit of *Talinum* (*Talinum*) *rivae* Chiov. is acropetally dehiscent (Carolin, in press; von Poellnitz, 1934b), but I suspect that this Somalian species actually belongs to *Calyptrotheca*. Acropetal dehiscence has been described for *Talinum paniculatum* (Jacq.) Gaertn. (Galati, 1986). According to Carolin (in press), the exocarp and endocarp in *Talinum* sect. *Talinum* sometimes separate (cf. Carolin, 1987). Carolin (1987) scored *Calandrinia* sect. *Monocosmia* as indehiscent, but elsewhere (Carolin, in press) reported occasional valvate dehiscence. Thus, I scored this section as dehiscent. Contrary to mine and Carolin's scores, Gerbaulet (1992) scored *Grahamia* for having a pericarp not differentiated into two layers.

I have disagreed (Hershkovitz, 1990a) with Carolin's (1987) interpretation of the pericarp of *Calandrinia* sect. *Calandrinia*: the distinctive "grooves and ribs" that characterize the capsule base of Montieae (Fig. 6) do not occur in the capsule base of any members of *C.* section *Calandrinia*. The capsule in the latter may, as Carolin (1987) noted, inroll after dehiscence (e.g., in *C. ciliata*; Fig. 7), but the capsule in *C. axilliflora* Barnéoud does not markedly inroll (Fig. 8). I scored *Calandrinia* as present for capsule valve inrolling and absent for capsule valve grooves and ribs. I scored indehiscent taxa and *Monocosmia* as unknown ("X") for character 41.

34. Fruit without acropetal, valvate dehiscence, 0; fruit with acropetal, valvate dehiscence, 1.
35. Fruit dehiscent, 0; fruit indehiscent, 1.
36. Fruit epidermal cells with sinuous radial walls, 0; fruit epidermal cells with straight walls, 1.
37. Fruit epidermal cells elongate, 0; fruit epidermal cells isodiametric, 1.
38. Pericarp not strongly differentiated into two layers, 0; pericarp strongly differentiated into two layers, 1.
39. Exocarp and endocarp not separating, 0; exocarp and endocarp separating, 1.
40. Exocarp not deciduous, 0; exocarp deciduous, 1.
41. Capsule valves not inrolling after dehiscence, 0; capsule valves inrolling after dehiscence, 1; fruit indehiscent, X.
42. Capsule valves not grooved and ribbed at the base, 0; Capsule valves grooved and ribbed at the base, 1.

SEEDS (CHARS. 43–44)

I have retained Carolin's (1987) characters, polarities, and scores for seed traits. As Carolin pointed out, however, the homology between the "aril" of *Talinum* sect. *Phemeranthus* and that of *Anacampseros* has not been established (see also Gerbaulet, 1992). I also note that many Portulacaceae have (usually less conspicuous) micropylar appendages (Corner, 1976; Hershkovitz, 1992), but I have not yet analyzed the variation in this feature.

←

the capsule base. B. Magnified view of capsule base showing grooves and ribs.—7. Dehisced capsule of *Calandrinia* (*Calandrinia*) *ciliata* [U.S.A., California: *Wolf 3542* (US)] showing capsule-valve inrolling. A grooved, ribbed base is not present. A sepal has been folded down to show the capsule base.—8. Partially dehisced capsule of *Calandrinia* (*Calandrinia*) *axilliflora* [Chile, Region Aconcagua: *Steudel s.n.* (P)]. Neither capsule-valve inrolling nor a grooved, ribbed capsule base is evident. Following dehiscence, the capsule valves may retain their shape or twist and fold irregularly. A sepal has been folded down to show the capsule base. G = groove, R = rib, S = sepal. Drawings by Leslie Randall.

9

FIGURE 9. Consensus tree of Portulacaceae as in Figure 1 but with nodes labeled for referencing Appendix 2.

43. Seeds without enveloping aril, 0; seeds with aril, 1.
44. Embryo encircling the perisperm, 0; embryo not encircling the perisperm, 1.

CHROMOSOME NUMBER (CHARS. 45, 46)

This character is added here based on data compiled and/or reported by Bernardello (1989), Hershkovitz (1992), Nilsson (1966b), Nyanyano (1986a), and Ford (1992; unpublished). The data are incomplete for most of the larger taxa. The base number 9 is tentatively presumed to be primitive because it is the most widespread among other Centrospermae (Ehrendorfer, 1976), but base numbers of 8 also occur among otherwise primitive Aizoaceae (Bittrich & Struck, 1989). The base number 8 occurs in derived species of *Portulaca* but is possibly primitive in *Claytonia* (see Gerbaulet, 1992, for discussion and references). Because of variability, I scored *Claytonia* as unknown. No ordering for base numbers of 10, 11, or 12 is supposed—these can all be derived from 9 via one step. My character definitions are faulty in treating nonequivalent states (i.e., 10, 11, and 12) as homologous. I resort to this treatment because the primitive base number in some well-surveyed taxa, e.g., *Lewisia* and *Montia*, is uncertain but clearly not 9. I scored *Cistanthe* sect. *Strophiolum* as unknown but not 9, but my conclusion that its base number is 11 or 12 is speculative (Hershkovitz, 1992). Gerbaulet (1992) reported $x = 9$ in *Talinaria*, which I scored as unknown. My consensus tree (Fig. 1), however, predicted $x = 9$ in this genus.

45. Chromosome base number 9, 0; chromosome base number not 9, 1.
46. Chromosome base number 10, 0; chromosome base number 11, 1; chromosome base number 12, 2; chromosome base number 9, X.

APPENDIX 2. Character state changes in the consensus tree. Listed below, by character number (cf. Appendix 1) and tree node (Fig. 9; cf. Fig. 1) are the character state changes of the consensus cladogram for Portulacaceae as output using PAUP's "list changes" option and "accelerated transition" optimization in the "describe trees" command. The number of changes listed is 114; hence the list includes excess homoplasious changes with respect to any 107-step resolution of the consensus tree. Unambiguous changes are shown in Figure 1. "CI" = consistency index.

| Character | CI | Steps | Changes |
|---|---|---|---|
| 1 | 0.500 | 1 | node 35 0 ⇒ 1 *Grahamia* |
| | | 1 | node 40 0 ⇒ 1 node 39 |
| 2 | 0.333 | 1 | node 40 1 ⇒ 0 node 37 |
| | | 1 | node 34 0 ⇒ 1 *Anacampseros* § *Tuberosae* |
| | | 1 | node 40 1 ⇒ 0 node 39 |
| 3 | 0.333 | 1 | node 42 0 ⇒ 1 node 41 |
| | | 1 | node 49 0 ⇒ 1 node 48 |
| | | 1 | node 51 0 ⇒ 1 *Montia* excl. § *Naiocrene* |
| 4 | 0.250 | 1 | node 46 0 ⇒ 1 node 40 |
| | | 1 | node 34 1 ⇒ 0 *Anacampseros* § *Anacampseros* |
| | | 1 | node 34 1 ⇒ 0 *Anacampseros* § *Avonia* |
| | | 1 | node 39 1 ⇒ 0 *Calyptrotheca* |
| 5 | 1.000 | 1 | node 37 0 ⇒ 1 node 36 |
| 6 | 0.500 | 1 | node 37 0 ⇒ 1 node 36 |
| | | 1 | node 34 1 ⇒ 0 *Anacampseros* § *Tuberosae* |
| 7 | 0.500 | 1 | node 35 0 ⇒ 1 *Talinopsis* |
| | | 1 | node 39 0 ⇒ 1 node 38 |
| 8 | 1.000 | 1 | node 46 1 ⇒ 0 node 40 |
| 9 | 1.000 | 1 | node 46 1 ⇒ 0 node 40 |
| 10 | 1.000 | 1 | node 46 0 ⇒ 1 node 40 |
| 11 | 0.200 | 1 | node 46 0 ⇒ 1 node 40 |
| | | 1 | node 35 1 ⇒ 0 node 34 |
| | | 1 | node 36 1 ⇒ 0 *Portulaca* |
| | | 1 | node 39 1 ⇒ 0 node 38 |
| | | 1 | node 50 0 ⇒ node 49 |
| 12 | 0.250 | 1 | node 36 0 ⇒ 1 *Portulaca* |
| | | 1 | node 37 0 ⇒ 1 *Talinum* § *Talinum* |
| | | 1 | node 38 0 ⇒ 1 *Ceraria* |
| | | 1 | node 52 0 ⇒ 1 node 50 |

APPENDIX 2. Continued.

| Character | CI | Steps | Changes |
|---|---|---|---|
| 13 | 0.333 | 1 | node 43 0 ⇒ 1 node 42 |
| | | 1 | node 42 1 ⇒ 0 *Calandrinia acaulis* |
| | | 1 | node 52 0 ⇒ 1 node 51 |
| 14 | 1.000 | 1 | node 43 1 ⇒ 0 node 42 |
| 15 | 0.500 | 1 | node 46 0 ⇒ 1 node 40 |
| | | 1 | node 37 1 ⇒ 0 *Schreiteria* |
| 16 | 0.333 | 1 | node 37 0 ⇒ 1 *Schreiteria* |
| | | 1 | node 43 0 ⇒ 1 node 42 |
| | | 1 | node 51 0 ⇒ 1 *Montia* § *Naiocrene* |
| 17 | 0.200 | 1 | node 34 0 ⇒ 1 *Anacampseros* § *Anacampseros* |
| | | 1 | node 34 0 ⇒ 1 *Anacampseros* § *Tuberosae* |
| | | 1 | node 37 0 ⇒ 1 *Talinum* § *Talinum* |
| | | 1 | node 46 0 ⇒ 1 node 45 |
| | | 1 | node 42 1 ⇒ 0 *Calandrinia acaulis* |
| 18 | 1.000 | 1 | node 45 0 ⇒ 1 node 44 |
| 19 | 1.000 | 1 | node 45 0 ⇒ 1 node 44 |
| 20 | 1.000 | 1 | node 45 0 ⇒ 1 node 44 |
| 21 | 1.000 | 1 | node 45 0 ⇒ 1 node 43 |
| 22 | 0.500 | 1 | node 36 1 ⇒ 0 *Portulaca* |
| | | 1 | node 40 1 ⇒ 0 node 39 |
| 23 | 0.400 | 1 | node 35 0 ⇒ 1 node 34 |
| | | 1 | node 40 0 ⇒ 1 *Rumicastrum* |
| | | 1 | node 45 0 ⇒ 2 node 44 |
| | | 1 | node 52 0 ⇒ 1 node 50 |
| | | 1 | node 52 0 ⇒ 1 node 51 |
| 24 | 0.333 | 1 | node 35 0 ⇒ 1 *Grahamia* |
| | | 1 | node 45 0 ⇒ 1 node 43 |
| | | 1 | node 52 0 ⇒ 1 *Lenzia* |
| 25 | 0.250 | 1 | node 45 0 ⇒ 1 node 43 |
| | | 1 | node 42 1 ⇒ 0 *Calandrinia acaulis* |
| | | 1 | node 42 1 ⇒ 0 *Calandrinia carolinii* |
| | | 1 | node 52 0 ⇒ 1 node 51 |
| 26 | 1.000 | 1 | node 51 0 ⇒ 1 node 50 |
| 27 | 0.250 | 1 | node 35 0 ⇒ 1 node 34 |
| | | 1 | node 36 0 ⇒ 1 *Portulaca* |
| | | 1 | node 37 0 ⇒ 1 *Talinum* § *Talinum* |
| | | 1 | node 40 0 ⇒ 1 *Talinum* § *Phemeranthus* |
| 28 | 0.500 | 1 | node 37 0 ⇒ 1 *Schreiteria* |
| | | 1 | node 52 0 ⇒ 1 *Lewisia* |
| 29 | 0.200 | 1 | node 42 0 ⇒ 1 *Calandrinia acaulis* |
| | | 1 | node 42 0 ⇒ 1 *Calandrinia carolinii* |
| | | 1 | node 42 0 ⇒ 1 *Calandrinia affinis* |
| | | 1 | node 50 0 ⇒ 1 *Cistanthe* § *Strophiolum* |
| | | 1 | node 52 0 ⇒ 1 *Lewisia* |
| 30 | 0.200 | 1 | node 52 0 ⇒ 1 node 46 |
| | | 1 | node 39 1 ⇒ 0 node 38 |
| | | 1 | node 44 1 ⇒ 0 *Montiopsis* § *Dianthoideae* |
| | | 1 | node 51 0 ⇒ 1 *Montia* § *Naiocrene* |
| | | 1 | node 51 0 ⇒ 1 *Montia* excl. § *Naiocrene* |
| 31 | 0.250 | 1 | node 37 0 ⇒ 1 *Schreiteria* |
| | | 1 | node 39 0 ⇒ 1 *Calyptrotheca* |
| | | 1 | node 45 0 ⇒ 1 node 43 |
| | | 1 | node 44 0 ⇒ 1 *Montiopsis* § *Montiopsis* |
| 32 | 0.333 | 1 | node 35 0 ⇒ 1 *Grahamia* |
| | | 1 | node 36 0 ⇒ 1 *Portulaca* |
| | | 1 | node 52 0 ⇒ 1 *Lewisia* |

APPENDIX 2. Continued.

| Character | CI | Steps | Changes |
|---|---|---|---|
| 33 | 0.500 | 1 | node 41 0 ⇒ 1 *Calandrinia* § *Monocosmia* |
| | | 1 | node 48 0 ⇒ 1 node 47 |
| 34 | 0.500 | 1 | node 39 0 ⇒ 1 *Calyptrotheca* |
| | | 1 | node 52 0 ⇒ 1 *Lewisia* |
| 35 | 0.500 | 1 | node 39 0 ⇒ 1 node 38 |
| | | 1 | node 47 0 ⇒ 1 *Cistanthe* § *Philippiamra* |
| 36 | 0.333 | 1 | node 40 0 ⇒ 1 node 37 |
| | | 1 | node 34 1 ⇒ 0 *Anacampseros* § *Tuberosae* |
| | | 1 | node 39 0 ⇒ 1 *Calyptrotheca* |
| 37 | 0.333 | 1 | node 36 0 ⇒ 1 node 35 |
| | | 1 | node 34 1 ⇒ 0 *Anacampseros* § *Tuberosae* |
| | | 1 | node 37 0 ⇒ 1 *Talinum* § *Talinum* |
| 38 | 1.000 | 1 | node 40 0 ⇒ 1 node 37 |
| 39 | 0.500 | 1 | node 35 0 ⇒ 1 node 34 |
| | | 1 | node 35 0 ⇒ 1 *Talinopsis* |
| 40 | 1.000 | 1 | node 35 0 ⇒ 1 node 34 |
| 41 | 0.500 | 1 | node 41 0 ⇒ 1 *Calandrinia* § *Calandrinia* |
| | | 1 | node 52 0 ⇒ 1 node 51 |
| 42 | 1.000 | 1 | node 52 0 ⇒ 1 node 51 |
| 43 | 0.500 | 1 | node 36 0 ⇒ 1 node 35 |
| | | 1 | node 40 0 ⇒ 1 *Talinum* § *Phemeranthus* |
| 44 | 1.000 | 1 | node 36 0 ⇒ 1 node 35 |
| 45 | 0.500 | 1 | root 0 ⇒ 1 node 52 |
| | | 1 | node 37 1 ⇒ 0 node 36 |
| 46 | 0.400 | 1 | node 52 1 ⇒ 2 node 46 |
| | | 1 | node 38 2 ⇒ 1 *Portulacaria* |
| | | 1 | node 41 2 ⇒ 1 *Calandrinia* § *Monocosmia* |
| | | 1 | node 45 2 ⇒ 0 node 44 |
| | | 1 | node 48 1 ⇒ 0 *Cistanthe* § *Amarantoideae* |

# LEAF MORPHOLOGY OF *CALANDRINIA* AND *MONTIOPSIS* (PORTULACACEAE)[1]

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ABSTRACT

*Calandrinia* sect. *Calandrinia*, *C.* sect. *Monocosmia*, and some species of *C.* sect. *Acaules* share identical leaf blade and petiolar morphology, fimbrial veins, predominantly brachytetracytic and staurocytic stomata surrounded by a cycle of subsidiary-like cells, and unicellular ribbed trichomes or papillar trichomes. Other species of *C.* sect. *Acaules* have irregularly brochidodromous venation without a fimbrial vein, predominantly brachyparacytic stomata, and/or no trichomes; venation and stomatal morphology in these species is similar to that found in *Montiopsis*. Leaves of *Montiopsis* lack petioles, have glandular or eglandular, uniseriate- and/or multiseriate-multicellular trichomes (although some examined specimens of *M.* subg. *Dianthoideae* appear to be glabrous), and generally have brachyparacytic stomata (although some examined specimens of subgenus *Dianthoideae* have a small proportion of brachytetracytic/staurocytic stomata with an outer cycle of cells). Leaves of *M.* subg. *Montiopsis* also have barbellate trichomes apparently composed of elongate hair cells, and have predominantly brachyparacytic or anomocytic stomata. Phylogenetic analysis of foliar characters of Portulacaceae: (1) supports a close relationship between *C.* sects. *Calandrinia* and *Monocosmia* and species of *C.* sect. *Acaules;* (2) indicates that *C.* sect. *Acaules* may be paraphyletic with respect to the preceding taxa; (3) provides weak evidence contradicted by nonfoliar evidence that *Claytonia* and *Montia* may be nested within *Calandrinia;* (4) provides weak evidence linking *Montiopsis* with *Calandrinia*; and (5) indicates that foliar characters may not be more homoplasious than nonfoliar. Phylogenetically analyzed systematic accounts of foliar morphology, such as that presented here, may provide a basis for advancing theories on the relationship between leaf form, function, and ontogeny.

In previous papers (Hershkovitz, 1991a, 1992), I demonstrated the utility of foliar morphology in clarifying phylogenetic relationships among members of Portulacaceae. The present paper presents and evaluates foliar morphological data for *Calandrinia* Kunth and *Montiopsis* Kuntze.

The circumscriptions of *Calandrinia* and *Montiopsis* accepted here are based on a cladistic reanalysis of Carolin's (1987) data for Portulacaceae that incorporates the leaf morphological evidence presented below (Hershkovitz, 1993). *Calandrinia* and *Montiopsis* include ca. 29 of the 100–150 species formerly classified in *Calandrinia* sensu lato. I had previously advocated retaining *Montiopsis* in *Calandrinia* (Hershkovitz, 1990; see also 1991b, fig. 3), but cladistic analysis does not strongly support this relationship (Hershkovitz, 1993). *Calandrinia*, as here circumscribed, includes ca. 14 species in three sections: (1) *C.* sect. *Calandrinia* (≡ *C.* sect. *Compressae* Reiche; including *C.* sect. *Axillares* Reiche; ca. 5 spp. of western America); (2) *C.* sect. *Acaules* Reiche (ca. 8 spp. of western South America and Mexico); and (3) *C.* sect. *Monocosmia* (Fenzl) Hershkovitz (1 sp. in Chile and Argentina). *Montiopsis* is restricted to temperate South America and includes two subgenera, *M.* subg. *Montiopsis* (≡ *Calandrinia* subg. *Hirsutae*; ca. 15 spp.) and *M.* subg. *Dianthoideae* (Reiche) D. I. Ford (ca. 3 spp.).

## MATERIALS AND METHODS

Gross leaf morphology, leaf venation pattern, and epidermal morphology were examined and photographed according to the protocols I described previously (Hershkovitz, 1991a). The morphology

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TABLE 1. Species, citations, and specimens examined for venation and epidermal features. Listed by genus, section, species, locality, collector, number, and herbarium are specimens of *Calandrinia* and *Montiopsis* prepared for venation ("v") and epidermal ("e") study. Specimens of *Calandrinia* sect. *Acaules* are identified according to the key in Table 2. Determinations of species for *Montiopsis* are fide Ford (1992). Specimens of *Montia* and *Rumicastrum* illustrated for foliar features are also cited. Locality information is limited to the largest political division within a country.

*Calandrinia* Kunth in HBK, Nov. Gen. Spec. 6: 77. 1823.

*Calandrinia* sect. *Calandrinia*. (≡ *Calandrinia* sect. *Compressae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.)

*C. alba* (Ruiz & Pavón) DC., Prodr. 3: 359. 1828. PERU. LA LIBERTAD: *Lopez 1223* (US), e.

*C. axilliflora* Barnéoud in Gay, Fl. Chile [Hist. Fisica y Politica de Chile, Botanica] 2: 486. 1847 ("1846"). CHILE. METROPOLITANA: *Joseph 2786* (US), e, v; *Philippi 697* (US), v; VALDIVIA: *Joseph 2728* (US), v.

*C. breweri* S. Watson, Proc. Amer. Acad. Arts 11: 124. 1876. U.S.A. CALIFORNIA: *Hoover 6697* (UC), e, v.

*C. ciliata* (Ruiz & Pavón) DC., Prodr. 3: 359. 1828. COLOMBIA. SANTANDER: *Araque & Barkley 18010* (US), v. GUATEMALA. HUEHUETENANGO: *Beaman 3102* (US), e. PERU. HUANCAVELICA: *Tovar 127* (US), v. U.S.A. CALIFORNIA: *Wolf 3453* (US), e, v; OREGON: *Maguire & Holmgren 26606* (US), v.

*C. compressa* Schrad. ex DC., Prodr. 3: 359. 1828. WITHOUT LOCALITY. *Gerhard s.n.* (B), v. CHILE. ACONCAGUA: *Joseph 4032* (US), v; MAULE: *Joseph 3720* (US), v.

*Calandrinia* sect. *Acaules* Reiche, Ber. Deutsch. Bot. Ges. 15:500. 1897.

*C. acaulis* Kunth in HBK, Nov. Gen. Spec. 6: 78. 1823.

*C. acaulis* var. *acaulis*. ARGENTINA. SALTA: *Venturi 7017* (US), v. BOLIVIA. LA PAZ: *Asplund 6289* (US), v. ECUADOR. PICHINCHA: *Heilborn 231* (US), v. MEXICO. MEXICO: *Beaman 1881* (F), v; *Pringle 4256* (US), v; *Balls 4247* (US), e. PERU. LIMA: *Cerrate 995* (US), v.

*C. acaulis* var. *magna* Macbride, Candollea 5: 350. 1934. PERU. LIMA: *Killip & Smith 21648* (US), e, v.

*C. affinis* Gillies ex Arn. in Cheek, Edinburgh J. Nat. Geogr. Sci. 1: 355. 1831. CHILE. WITHOUT LOCALITY: *Reiche s.n.* (B), e; MAULE: *Werdermann 606* (F), v; METROPOLITANA: *Hastings 497* (US), v; *Mahu 10998* (UC), v.

*C. caespitosa* Gillies ex Arn. in Cheek, Edinburgh J. Nat. Geogr. Sci. 1: 356. 1831. ARGENTINA. CHUBUT: *Beetle 351* (US), v; NEUQUEN: *Rossow 1084* (NA), e; *Schjovskoy s.n.* (M), e, v; SANTA CRUZ: *Sleumer 853* (US), v; *Sleumer 967* (US), v. CHILE. ACONCAGUA: *Buchtien s.n.* (US), e, v.

*C. carolinii* Hershkovitz & Ford, Phytologia 74: 282. 1993. ARGENTINA. CATAMARCA: *Jorgensen 1200* (US), e; JUJUY: *Venturi 8786* (US), e, v; SALTA: *Venturi 7018* (US), e; *Venturi 8538* (US), v; TUCUMAN: *Venturi 4824* (US), e, v.

*C. colchaguensis* Barnéoud in Gay, Fl. Chile [Hist. Fisica y Politica de Chile, Botanica] 2: 483. 1847 ("1846"). CHILE. ARAUCANIA: *Eyerdam 10239* (UC, US), e, v; BIO-BIO: *Germain s.n.* (US), v; *Werdermann 1325* (US), e.

*C. compacta* Barnéoud in Gay, Fl. Chile [Hist. Fisica y Politica de Chile, Botanica] 2: 481. 1847 ("1846"). ARGENTINA. SALTA: *Venturi 9239* (US), v. CHILE. ANTOFAGASTA: *Werdermann 1035* (US), e; ATACAMA: *Werdermann 952* (US), v.

*C. graminifolia* Phil., Linnaea 28: 690. 1856. ARGENTINA. NEUQUEN: *Arroyo & Leuenberger 3438* (B), e, v. CHILE. MAULE: *Philippi 291* (B), e, v.

*Calandrinia* sect. *Monocosmia* (Fenzl in Endl. & Fenzl) Hershkovitz, Phytologia 70: 223. 1991.

*C. monandra* (Ruiz & Pavón) DC., Prodr. 3: 359. 1828. ARGENTINA. RIO NEGRO: *Buchtien 37* (US), v. CHILE. ACONCAGUA: *Joseph 3719* (US), e, v.

*Montiopsis* Kuntze, Rev. Gen. Pl. 3(2): 14. 1898.

*Montiopsis* subg. *Montiopsis* (≡ *Calandrinia* subg. *Hirsutae* Reiche, Ber. Deutsch. Bot. Ges. 15: 502. 1897.).

*M. cumingii* (Hook. & Arn.) D. I. Ford, Phytologia 74:275. 1993. BOLIVIA. LA PAZ: *Asplund 4866* (US), e, v.

*M. capitata* (Hook. & Arn.) D. I. Ford, Phytologia 74: 274. 1993. ARGENTINA. RIO NEGRO: *Fischer 169* (US), e, v; SANTA CRUZ: *Sleumer 1166* (US), v. CHILE. ATACAMA: *Joseph 5123* (US), v; COQUIMBO: *Joseph 4505* (US), v.

*M. copiapina* (Phil.) D. I. Ford, Phytologia 74: 275. 1993. CHILE. ATACAMA: *Johnston 6069* (US), e, v.

*M. gilliesii* (Hook. & Arn.) D. I. Ford, Phytologia 74: 275. 1993. CHILE. ACONCAGUA: *Buchtien 1149* (L), e, v.

*M. parviflora* (Phil.) D. I. Ford, Phytologia 74: 276. 1993. CHILE. ATACAMA: *Johnston 5882* (US), e, v.

*M. uspallatensis* (Barnéoud) D. I. Ford, Phytologia 74: 276. 1993. CHILE. COQUIMBO: *Looser 2176* (US), v.

*M. trifida* (Hook. & Arn.) D. I. Ford, Phytologia 74: 276. 1993. CHILE. ANTOFAGASTA: *Johnston 3592* (F), v; COQUIMBO: *Joseph 4817* (US), v; *Rose & Rose 19254* (US), v.

*M. umbellata* (Ruiz & Pavón) D. I. Ford, Phytologia 74: 276. 1993. CHILE. BIO-BIO: *Joseph 3856* (US),

TABLE 1. Continued.

TABLE 1. Continued.

e, v; MAULE: *Grau & Grau 1516* (M), v; *Werdermann 586* (US), v; METROPOLITANA: *Kuntze s.n.* (US), v.

*Montiopsis* subg. *Dianthoideae* (Reiche) D. I. Ford, Phytologia 74: 277. 1993.

*M. andicola* (Gillies ex Hook.) D. I. Ford, Phytologia 74: 277. 1993. CHILE. METROPOLITANA: *Hastings 470* (US), v; *Hastings 488* (UC, US), e, v; *Hastings 489* (US), v; *Philippi 698* (US), v; O'HIGGINS: *Aravena 33356* (UC), v; *Bastin 17* (US), v.

*M. gayana* (Barnéoud) D. I. Ford, Phytologia 74: 277. 1993. ARGENTINA. RIO NEGRO: *Buchtien 36* (US), v; SANTA CRUZ: *Sleumer 1248* (US), e, v. CHILE. ARAUCANIA: *Werdermann 1219* (US), e, v; BIO-BIO: *Joseph 3496* (US), e, v; MAULE: *Joseph 5285* (US), v.

*M. cistiflora* (Gillies ex Arn.) D. I. Ford, Phytologia 74: 277. 1993. CHILE. MAULE: *Joseph 5615* (US), v; O'HIGGINS: *Philippi s.n.* (B), e, v.

*Montia* L., Sp. Pl. 87. 1753; Gen. Pl., ed. 5: 38. 1754.

*M. parvifolia* (Moç. ex DC.) Greene, Fl. Francisc. 181. 1891. CANADA. BRITISH COLUMBIA: *Calder et al. 14865* (US), e. U.S.A. CALIFORNIA: *Condit s.n.* (UC), v; *Randall s.n.* (UC), e, v; *Thomas 3542* (US), v.

*Rumicastrum* Ulbr. in Engler & Prantl, Nat. Pflanzenfam., 2 Aufl., 16c: 519. 1934.

*Rumicastrum* sp. WITHOUT DATA: Walter Kelley cleared leaf collection, no. K-242.

is described according to the terminology suggested by Dilcher (1974) for leaf size and shape, Hickey (1979) for venation pattern, Wilkinson (1979) for stomatal configuration, and Kelley (1973) for trichomes. The data presented here are supplemented with data from Becker (1895), Carolin (1987), Ford (1992), Kelley (1973), Nyanyano (1986a, b), and Peralta (1988). Table 1 lists the species, their full citations, and representative specimens. All specimens examined for epidermal and venation features are listed. Also listed are species, citations, and specimens of other Portulacaceae here illustrated.

Since submitting the morphological data presented here as part of a dissertation (Hershkovitz, 1990), I have substantially revised my taxonomic opinions on the species of *Calandrinia* sects. *Calandrinia* and *Acaules*. I previously treated *Calandrinia compressa* Schrad. ex DC. as a synonym of *C. ciliata* (Ruiz & Pavón) DC., but the former, restricted to Chile, is distinguished by its strongly compressed calyx of deltoid sepals. *Calandrinia ciliata*, apparently largely extra-Chilean, has a more campanulate calyx and more ovate sepals. Both species, however, are highly polymorphic, and several segregates have been described for each (cf. Reiche, 1898; Rydberg, 1932: 291, spp. 2–10).

The taxonomy of *Calandrinia* sect. *Acaules* is more complex and less satisfactory. Table 2 presents a revised, but still tentative, key to the species. Part of the confusion in my earlier work (Hershkovitz, 1990) stems from the "disappearance" of *Baitaria acaulis* Ruiz & Pavón from the floristic literature and/or the assumption that this name was synonymous with *Calandrinia acaulis* Kunth. Syntypes of *Baitaria acaulis* reportedly

TABLE 2. Provisional key to the species of *Calandrinia* sect. *Acaules* Reiche.

1a. Peduncles jointed; inflorescence bracts 2, foliaceous, attached above the middle of the peduncle.
  2a. Stamens 5–10; capsule usually membranous at maturity; leaves without trichomes or papillar trichomes (Ecuador, Colombia, Mexico, Venezuela) or occasionally with papillar trichomes along the leaf margin (Argentina, Bolivia, Peru).
    3a. Flowers ≤1 cm long ..... *C. acaulis* var. *acaulis*
    3b. Flowers ca. 2 cm long ..... *C. acaulis* var. *magna*
  2b. Stamens 12–20; capsule usually indurate at maturity; leaves often with trichomes or papillar trichomes ..... *C. carolinii*
1b. Peduncles not jointed; inflorescence bracts none or 2, scalelike and attached near the base of the peduncle, or 2, one scalelike, basal and one foliaceous, attached more apically
  4a. Inflorescence bracts 2.
    5a. Inflorescence ≤half as long as leaves, stamens ca. 8. ..... *C. colchaguensis*
    5b. Inflorescence >half as long as leaves, stamens >20.
      6a. Leaves linear-oblanceolate, flat, more than twice as broad as thick, glabrous or with trichomes or papillar trichomes along the leaf margin. ..... *C. affinis*
      6b. Leaves linear-filiform, ca. as broad as thick, with extra-marginal trichomes or papillar trichomes ..... *C. graminifolia*
  4b. Inflorescence bracts none.
    7a. Peduncles longer than leaves.
      8a. Stamens 6–7, petals pink to white ..... *C. fuegiana*
      8b. Stamens more than 7, petals rose, orange, or yellow ..... *C. caespitosa*
    7b. Peduncles shorter than leaves ..... *C. compacta*

include some plants of *Calandrinia acaulis*. The former species is now *Calandrinia carolinii* Hershkovitz & Ford (Hershkovitz & Ford, 1993). Plants of *C. carolinii* have usually been misidentified as *C. acaulis*. Realizing this error, I had mistakenly referred them to *C. colchaguensis* Barnéoud (Hershkovitz, 1990: 242). Likewise, I referred bona fide material of *C. colchaguensis* to *C. affinis* Gillies ex Arn. The last two species are very similar, however, and intergrade in their overlapping range (D. I. Ford, pers. comm.). I also referred to *Calandrinia compacta* Barnéoud diminutive Bolivian plants of *C. acaulis*. I previously recognized, primarily on geographical bases, *C. megarhiza* Hemsley (Central America) and *C. saltensis* Hauman (Argentina), as distinct from *C. acaulis* (South America). I now believe such distinctions are not warranted. *Calandrinia megarhiza* and *C. saltensis*, which represent the range extremes of *C. acaulis*, are distinguishable from one another by the presence of trichomes and slightly higher stamen number of *C. saltensis*. These traits are variable, however, in *C. acaulis* from Peru and Bolivia. Finally, I previously included *Calandrinia fuegiana* Gand. in *C. caespitosa* Gillies ex Arn. (cf. Peralta, 1988). I now recognize the former as distinct, although I have no leaf anatomical data for the species.

Identification of specimens of *Montiopsis* subg. *Dianthoideae* follows Peralta (1988), except that I refer *M. hirtella* Philippi to *M. gayana* (D. I. Ford, pers. comm.). Identification of specimens of *Montiopsis* subg. *Montiopsis* follows Ford (1992).

In order to evaluate the systematic significance of the foliar morphological data presented here, I reanalyzed my earlier PAUP analysis of Portulacaceae (Hershkovitz, 1993), comparing results generated by variously weighting and excluding foliar and nonfoliar characters. The data and character analyses are from Hershkovitz (1993, table 3, appendix 1).

## Results

### A. Leaf Morphology

*1. Gross leaf morphology.* The gross leaf morphology in *Calandrinia* and *Montiopsis* can be discerned from the illustrations of cleared leaves (Figs. 1–30, see below).

Leaves of *C.* sect. *Calandrinia* are mostly 10–70 mm long and 2–15 mm wide (nanophyllous to microphyllous; Dilcher, 1974); the basal leaves are usually larger than the cauline leaves. Within these size parameters, leaf shape varies from linear to oblanceolate or, when the lower portion of the leaf is more abruptly constricted into a winged petiole, often rhombic, ovate, or deltoid above the point of constriction and attenuated below (e.g., *C. axilliflora*, Fig. 1).

Leaves in *C.* (*Monocosmia*) *monandra* (Fig. 5) are ca. 25 mm long and 8 mm wide, generally wide-petiolate, rhombic above the point of constriction, and grossly indistinguishable from similarly sized and shaped leaves in *C.* sect. *Calandrinia*.

Leaves in *C.* sect. *Acaules* (Figs. 6, 9, 12, 15, 18) are all basal and exhibit a similar morphological range to those in *C.* sect. *Calandrinia*, but they are indistinctly to not at all petiolate, perhaps more succulent (although not readily evaluated from herbarium specimens), and/or much longer (up to 150 mm in *C. acaulis* var. *magna*).

Leaves in *Montiopsis* subgenera *Dianthoideae* (Figs. 19, 20, 23, 24) and *Montiopsis* (Figs. 27, 28) are usually 3–20(–40) mm long and usually less than 3 mm wide (leptophyllous to nanophyllous; Dilcher, 1974), usually oblanceolate to linear, and sessile or with a weakly defined petiolar region between the clasping leaf base and lamina. The leaf base margins in some specimens of *M. andicola* (Fig. 19) and *M. gayana* (subg. *Dianthoideae*) are irregularly dentate. The dentations intergrade with marginal trichomes toward the leaf apex (see below). Slight degrees of dentation also occur in conjunction with trichomes in *M.* subg. *Montiopsis*.

The leaf bases in all members of *Calandrinia* and *Montiopsis* are flattened, somewhat clasping to nearly sheathing, and not obviously jointed at the abscission zone.

*2. Leaf venation pattern.* Figures 1–30 illustrate gross leaf venation patterns of *Calandrinia* and *Montiopsis*; for comparative purposes, Figure 31 illustrates venation in *Montia parvifolia*. Figures 32–37 illustrate fine venation of *C.* sects. *Calandrinia*, *Monocosmia*, and *Acaules*. Figures 38–41 illustrate leaf apical venation in *C.* (*Calandrinia*) *axilliflora*, *C.* (*Monocosmia*) *monandra*, *C.* (*Acaules*) *carolinii*, and *Montia parvifolia*. The descriptions presented here are based on studies of over 150 cleared leaves from 65 individuals of ca. 23 species that represent the gross morphological extremes in *Calandrinia* and *Montiopsis* as evident from herbarium specimens. My comparisons of the data are based on examination of ca. 1,500 cleared leaves representing nearly all

species or species groups of Portulacaceae and ca. 500 additional cleared leaves from ca. 250 selected species throughout Centrospermae.

Venation in *C.* sect. *Calandrinia* (Figs. 1–5, 32, 33, 38) is characterized by a primary vein that is prominent basally but much diminished toward the leaf apex (Fig. 3) or distinct but ramified at the extreme apex (Fig. 38); secondary veins and prominent distal ramifications thereof that form indistinct loops ("arches"; cf. Hickey, 1979) near the leaf margin (Figs. 2, 4) or merge with the fimbrial vein (Fig. 1; see also below); and tertiary veins (sometimes constituting the highest distinct vein order, e.g., in Figs. 1, 32) that reticulate irregularly and/or give rise to freely ending veinlets (Fig. 32) or, in larger leaves, to a fourth order of reticulating veins (Fig. 32).

Areolation is imperfect; the areoles are variably sized and irregularly shaped (Figs. 32, 33) but, in contrast to Hickey's (1979) characterization of imperfect areolation, there are relatively few freely ending veinlets: the ultimate vein-enclosures usually contain no veinlets or one, usually unbranched, veinlet. A statistical study of the number and distribution of freely ending veinlets per ultimate vein enclosure, a potentially useful taxonomic character in *Calandrinia*, was not undertaken.

The marginal venation in leaves of *C.* sect. *Calandrinia* is characterized by a fimbrial vein (= a contiguous vein following the leaf margin; Figs. 1–4, 38), which is only weakly consolidated in the basal portion of the leaf but exceedingly prominent toward the leaf apex, where it becomes perpendicular to and overtops the primary vein (Fig. 37).

Leaf venation in *C.* sect. *Monocosmia* (Figs. 5, 34, 39) is, in all respects, indistinguishable from that in *C.* sect. *Calandrinia*.

Some species of *C.* sect. *Acaules* possess a fimbrial vein similar to that in *C.* sect. *Calandrinia*, e.g., *C. affinis* (Figs. 6–8, 35), *C. acaulis*, *C. acaulis* var. *magna* (Figs. 9–11, 36), and *C. carolinii* (Figs. 12–14, 37, 40). Other taxa lack a fimbrial vein, e.g., *C. compacta* (Figs. 15, 16), *C. caespitosa* (Figs. 17, 18), and some specimens of *C. affinis*. A fimbrial vein is weakly evident in small-leaved specimens of *C. acaulis* from Bolivia and Peru and the single examined specimen from Argentina ("*C. saltensis*"). In general, the fimbrial vein is less well consolidated in *C.* sect. *Acaules* (especially in *C. carolinii*; Figs. 12–14, 37, 40) than in *C.* sects. *Calandrinia* and *Monocosmia* but, as in the last sections, it becomes perpendicular to and overtops the primary vein at the leaf apex (Fig. 40). The primary vein in *C.* sect. *Acaules* is more or less distinct at the leaf apex (Fig. 10) or ramified at the extreme apex as in *C.* sects. *Calandrinia* and *Monocosmia* (Figs. 7, 13, 16, 17; especially evident in Fig. 40).

Otherwise, venation in *C.* sect. *Acaules* appears less well organized than in *C.* sect. *Calandrinia*. The secondary veins, especially toward the leaf apex, may merge with the fimbrial vein (Figs. 7, 10); toward the leaf base, the secondary veins form distinct secondary loops within the confines of the fimbrial vein (Figs. 8, 11, 14, 35–37). In leaves lacking a fimbrial vein, the secondary veins form

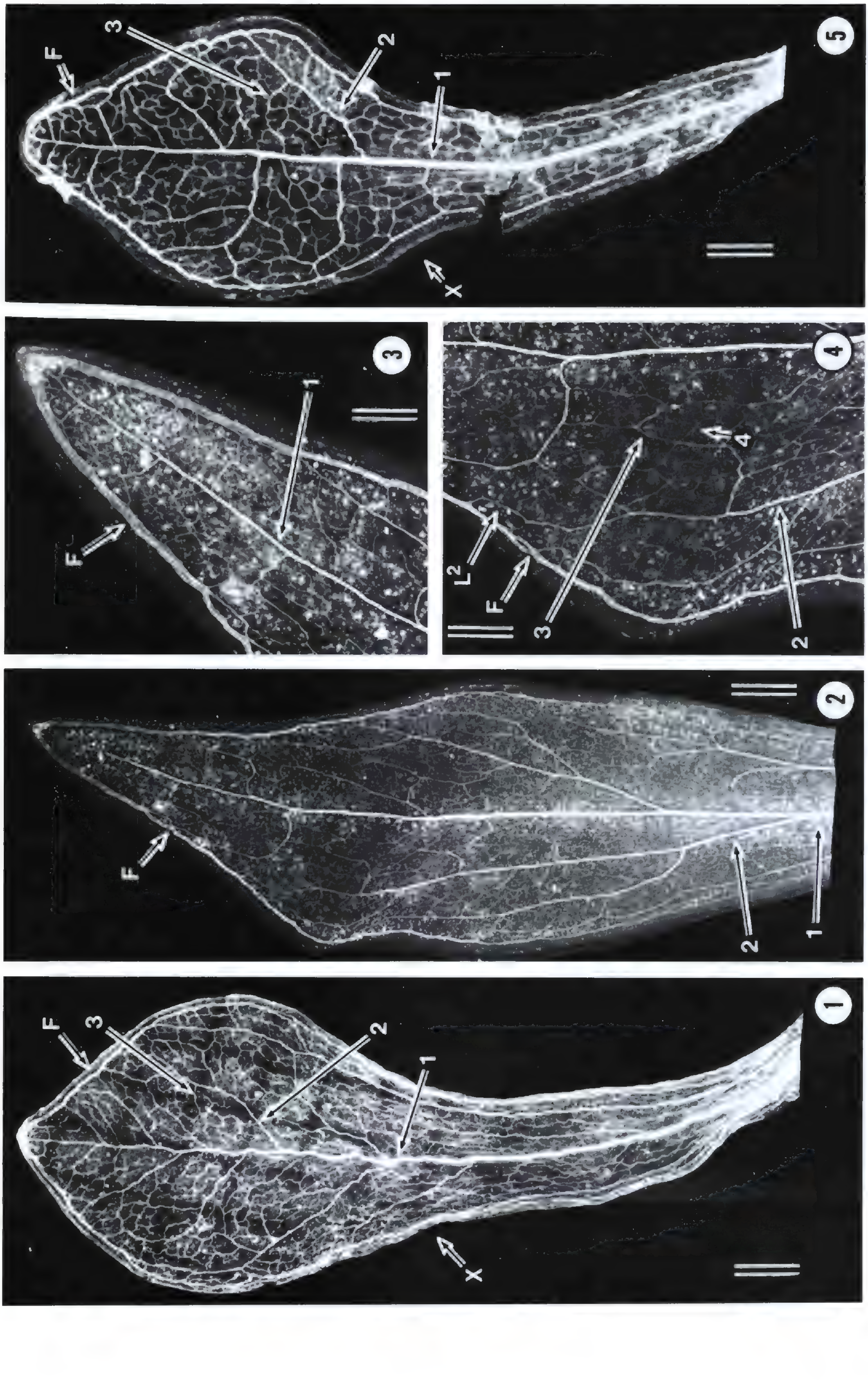
→

FIGURES 1–5.[3] Cleared leaves of *Calandrinia* sects. *Calandrinia* and *Monocosmia*. X, approximate position of the constriction between leaf blade and petiole.—1. Whole leaf of *C.* (*Calandrinia*) *axilliflora* (*Joseph 2786*). 2–4. *C.* (*Calandrinia*) *breweri* (*Hoover 6697*).—2. Leaf blade.—3. Leaf apex.—4. Midlaminal/marginal portion.—5. Whole leaf of *C.* (*Monocosmia*) *monandra* (*Buchtien 37*). Scale bars are (mm) ca. 1.6, 1.9, 1.2, 1.2, and 1.0, respectively.

FIGURES 6–14.[3] Cleared leaves of *Calandrinia* sect. *Acaules*. 6–8. *C. affinis* (*Werdermann 606*).—6. Leaf blade.—7. Leaf apex.—8. Midlaminal/marginal portion. 9–11. *C. acaulis* var. *magna* (*Killip & Smith 21648*).—9. Leaf blade.—10. Leaf apex.—11. Midlaminal/marginal portion. 12–14. *C. carolinii* (*Venturi 4824*).—12. Leaf blade.—13. Leaf apex.—14. Midlaminal portion. Scale bars are (mm) ca. 1.8, 0.8, 0.8, 3.2, 1.1, 1.1, 1.4, 0.7, and 0.2, respectively.

FIGURES 15–22.[3] Cleared leaves of *Calandrinia* sect. *Acaules* and *Montiopsis* subg. *Dianthoideae*. 15, 16. *C.* (*Acaules*) *compacta* (*Werdermann 952*).—15. Leaf blade.—16. Leaf apex. 17, 18. *C.* (*Acaules*) *caespitosa* (*Schjovskoy s.n.*).—17. Leaf blade.—18. Leaf apex.—19. Leaf blade of *M.* (*Dianthoideae*) *andicola* (*Bastin 17*). Note dentations near the leaf base, two of which are vascularized (X). 20–22. *M. andicola* (*Aravena 33356*).—20. Leaf blade.—21. Leaf apex.—22. Midlaminal/marginal portion. Scale bars are (mm) ca. 1.2, 0.7, 0.9, 1.8, 0.8, 1.4, 0.6, and 0.6, respectively.

[3] FIGURES 1–37. Cleared leaves of *Calandrinia*, *Montiopsis*, and *Montia parvifolia*. Vouchers are listed in Table 1. 1, primary vein; 2, secondary vein; etc.; $L^2$, secondary loop; F, fimbrial vein.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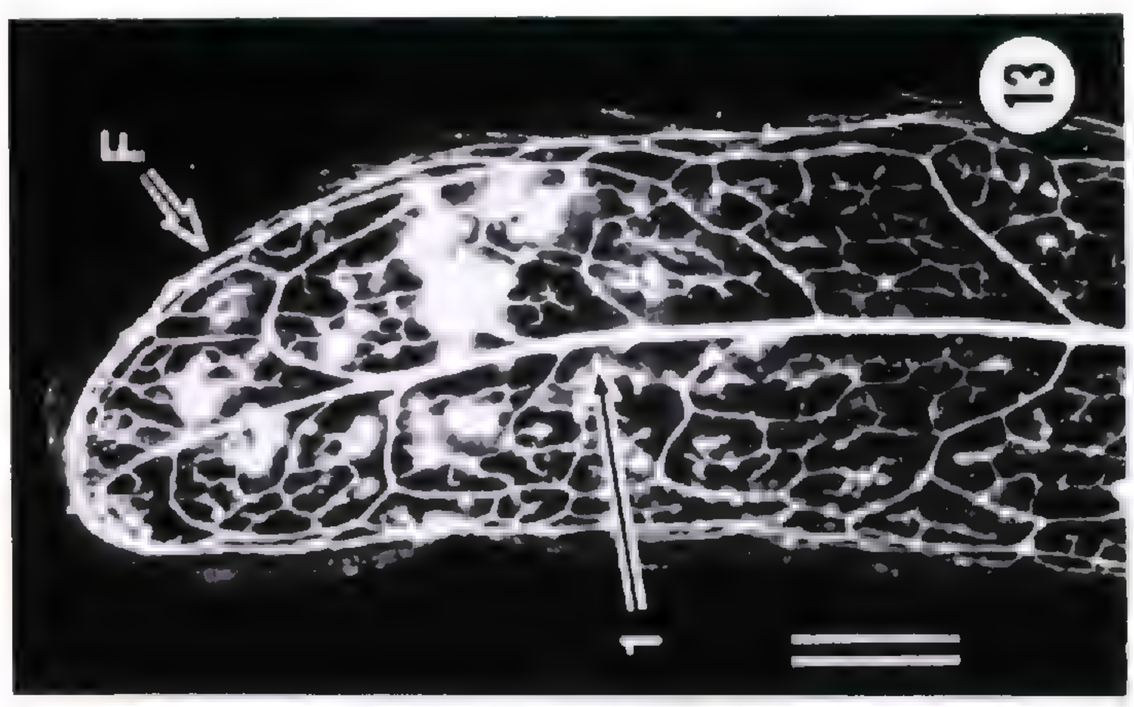
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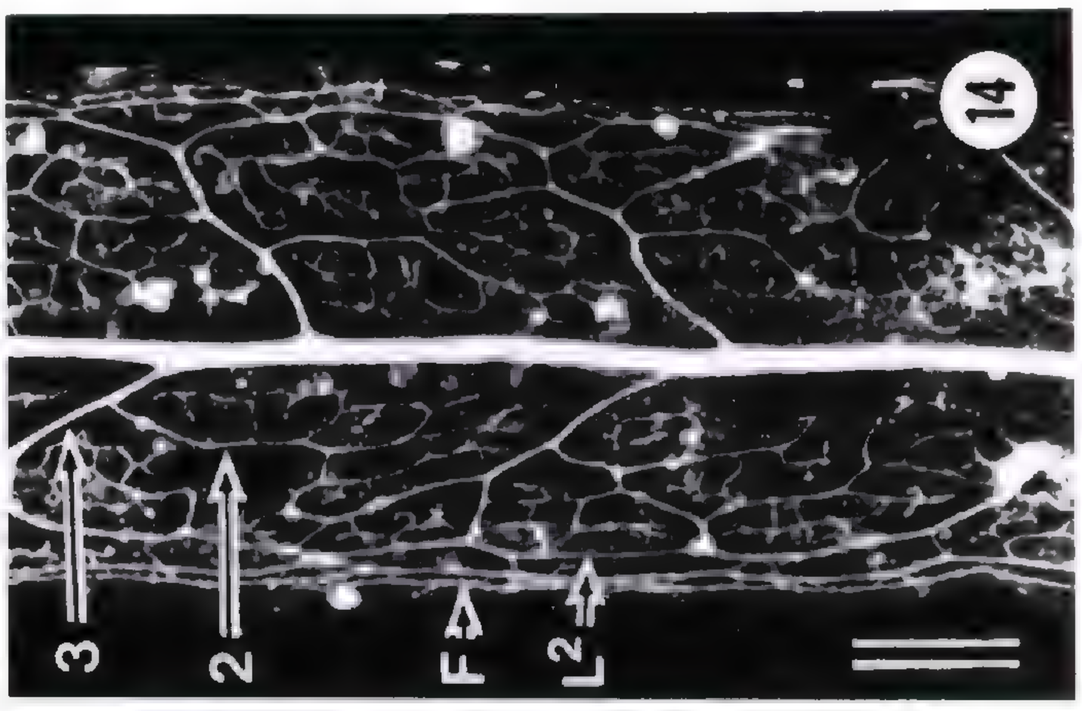
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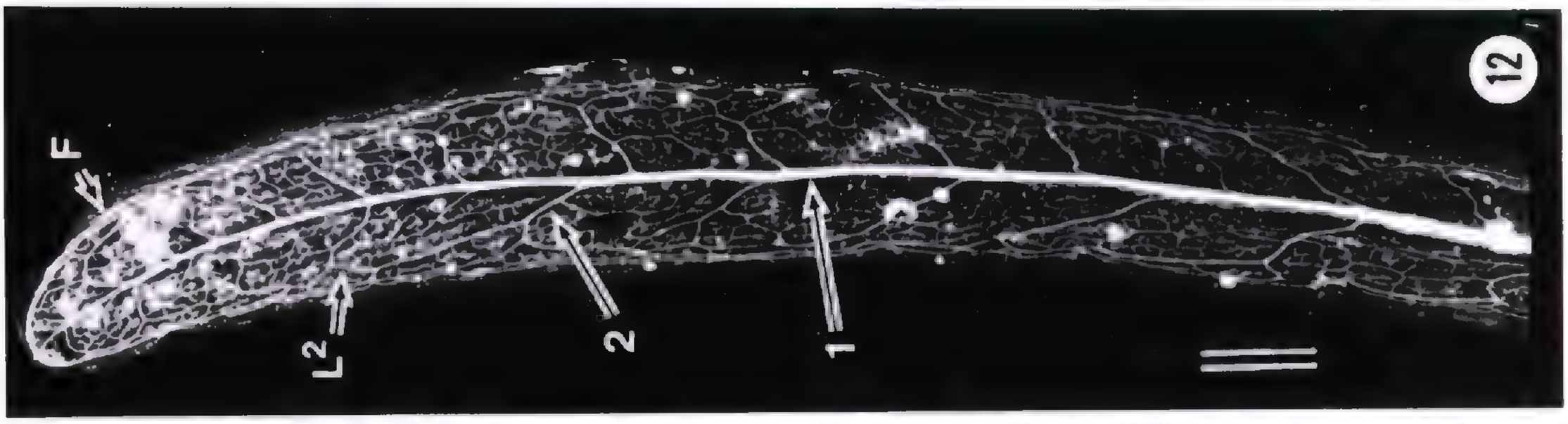
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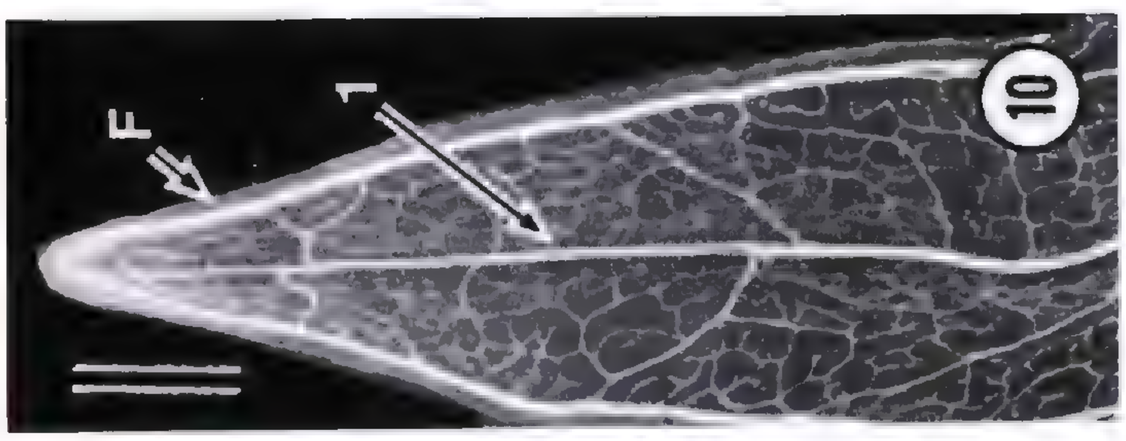
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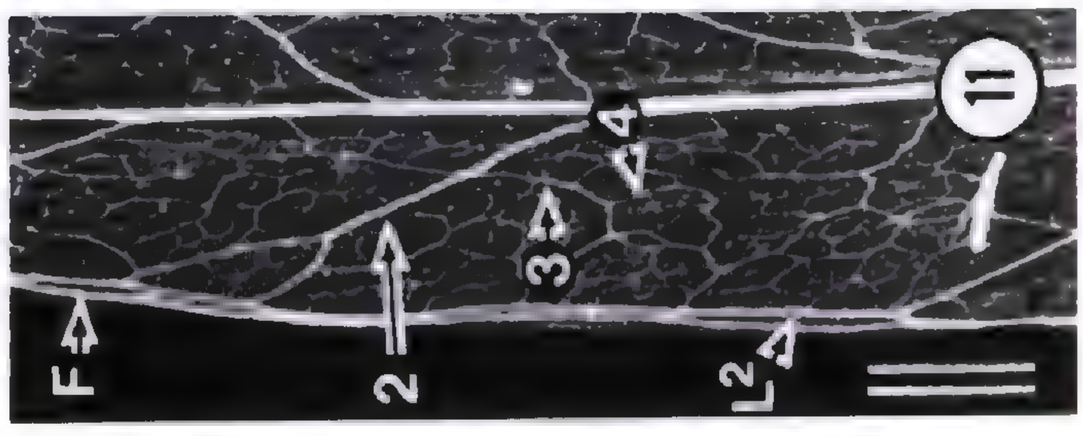
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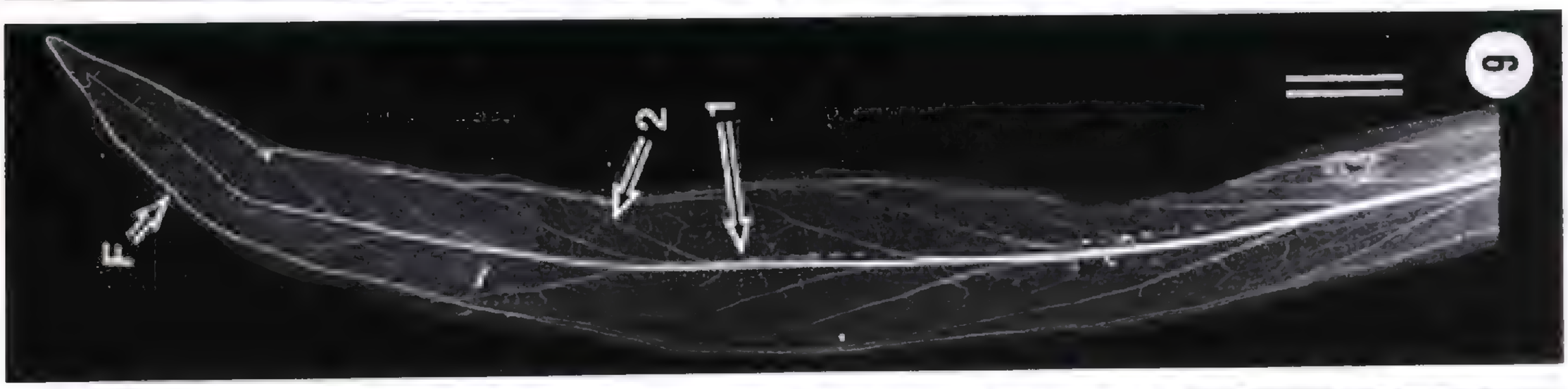
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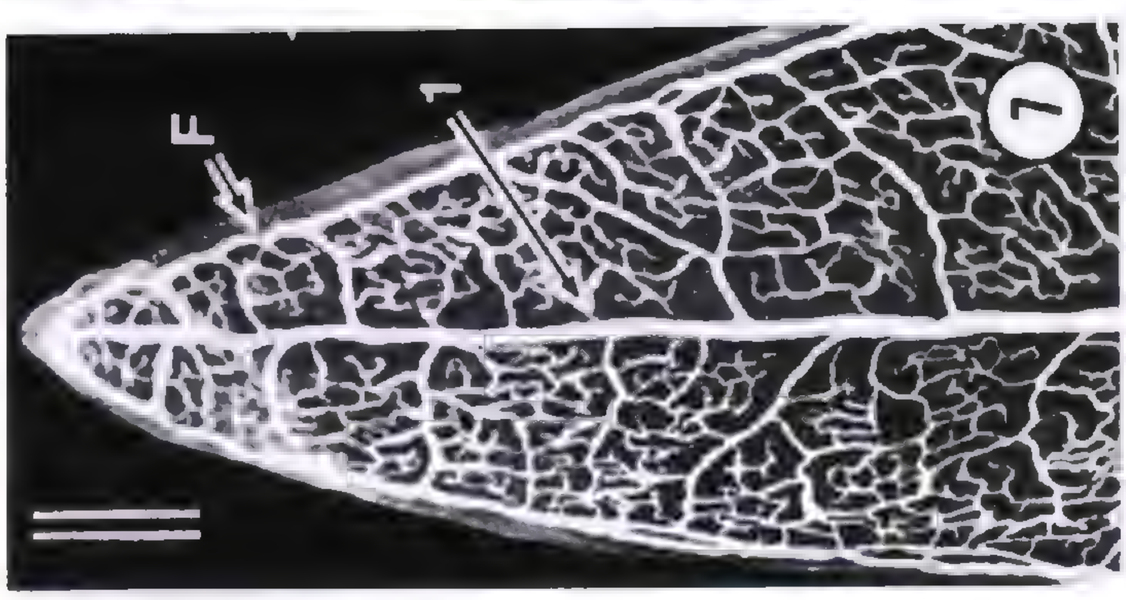
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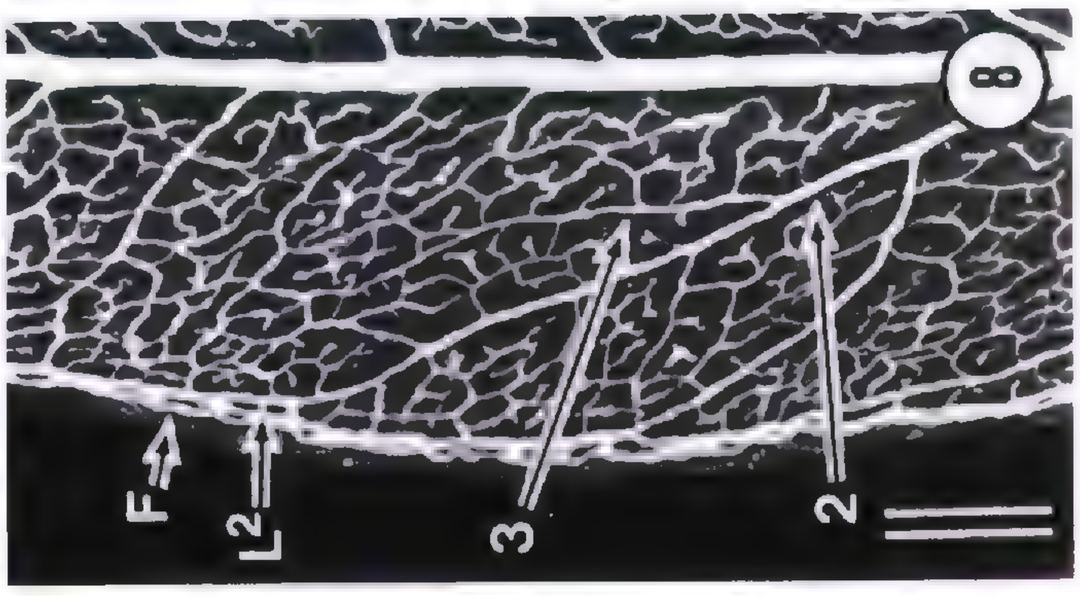
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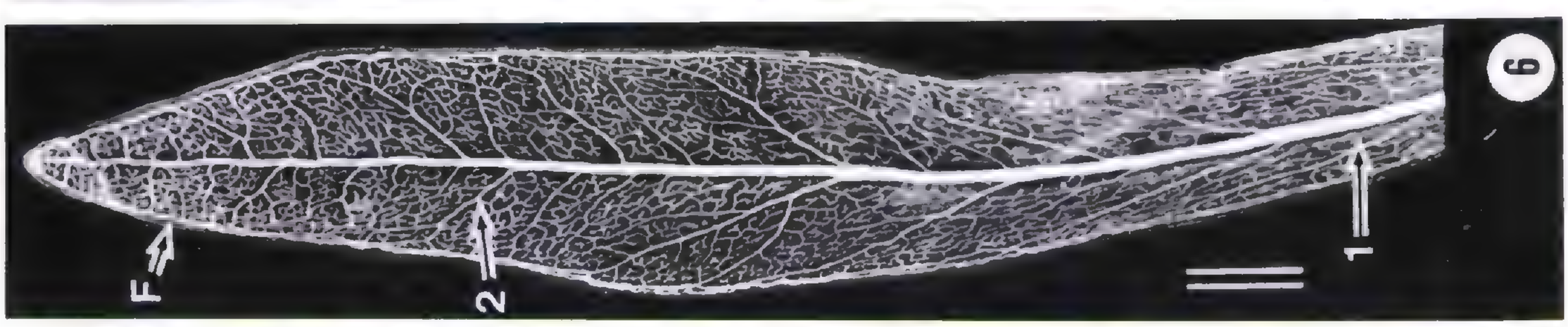
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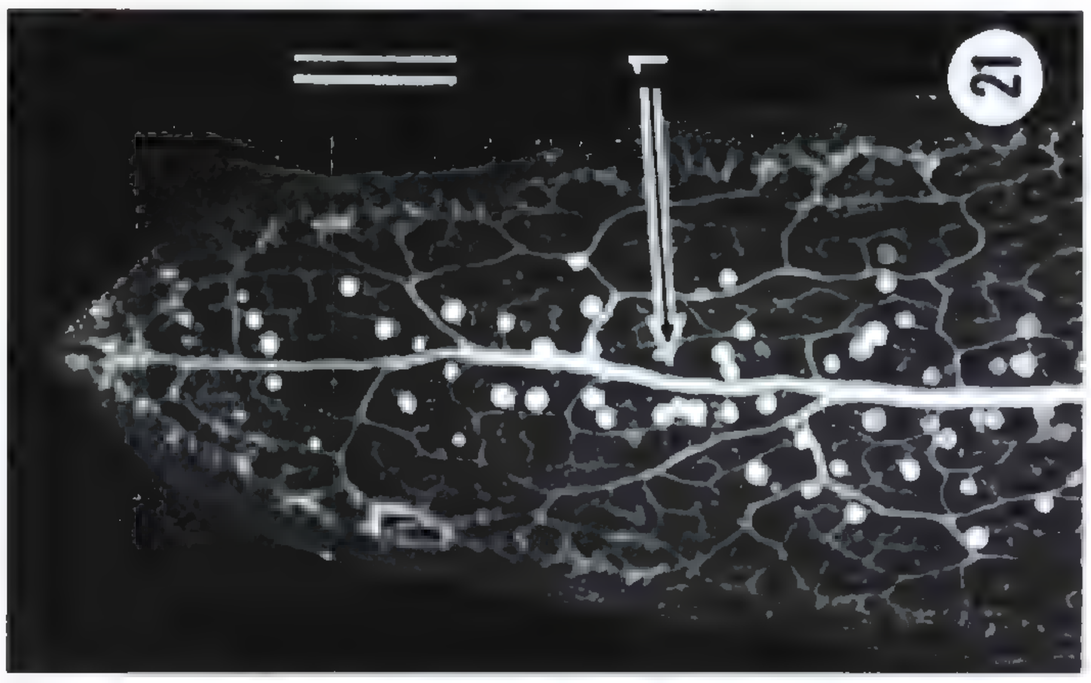
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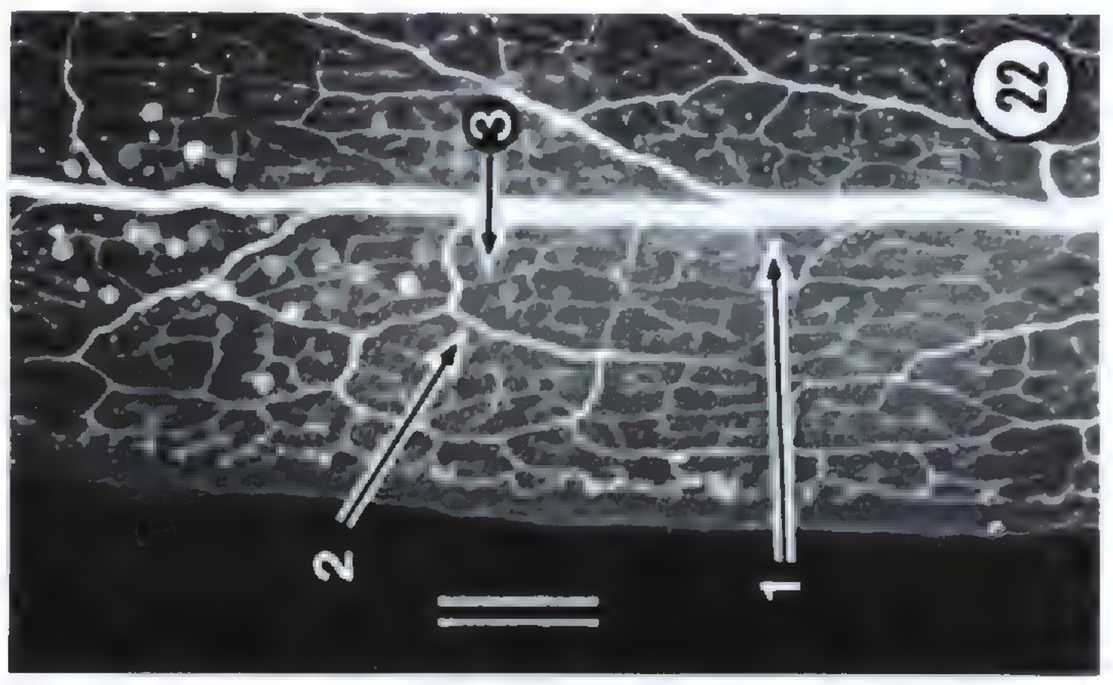
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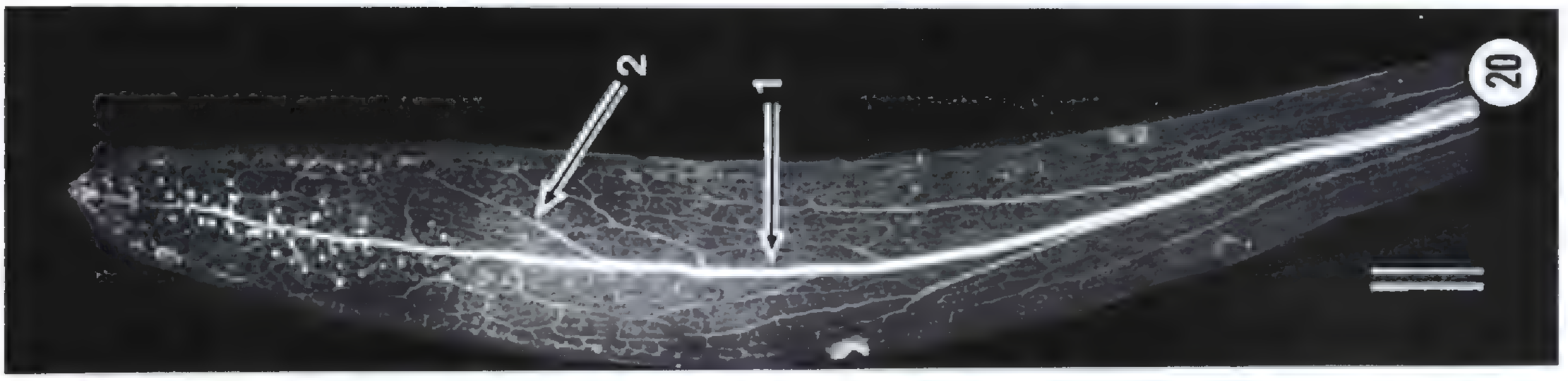
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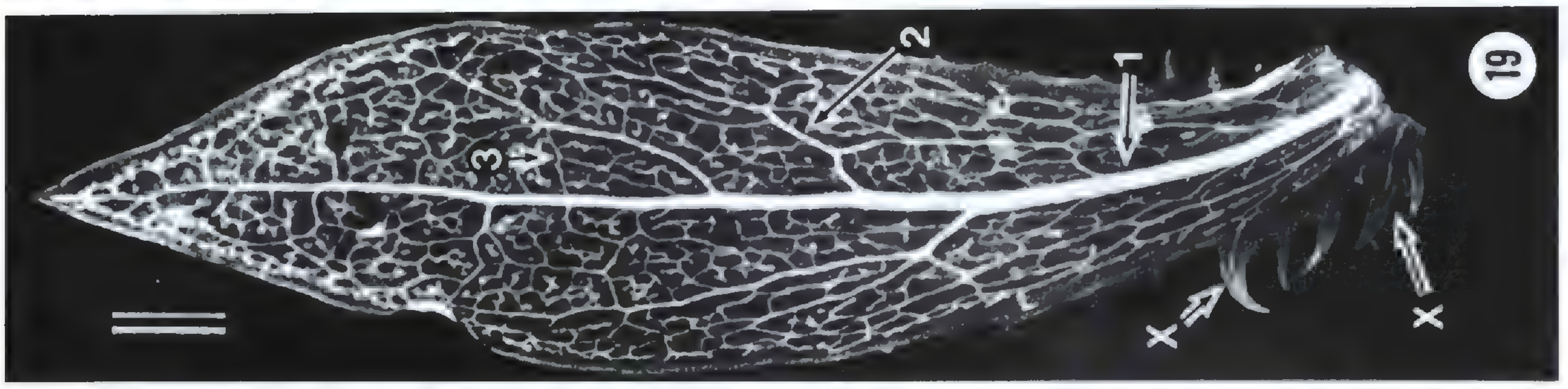
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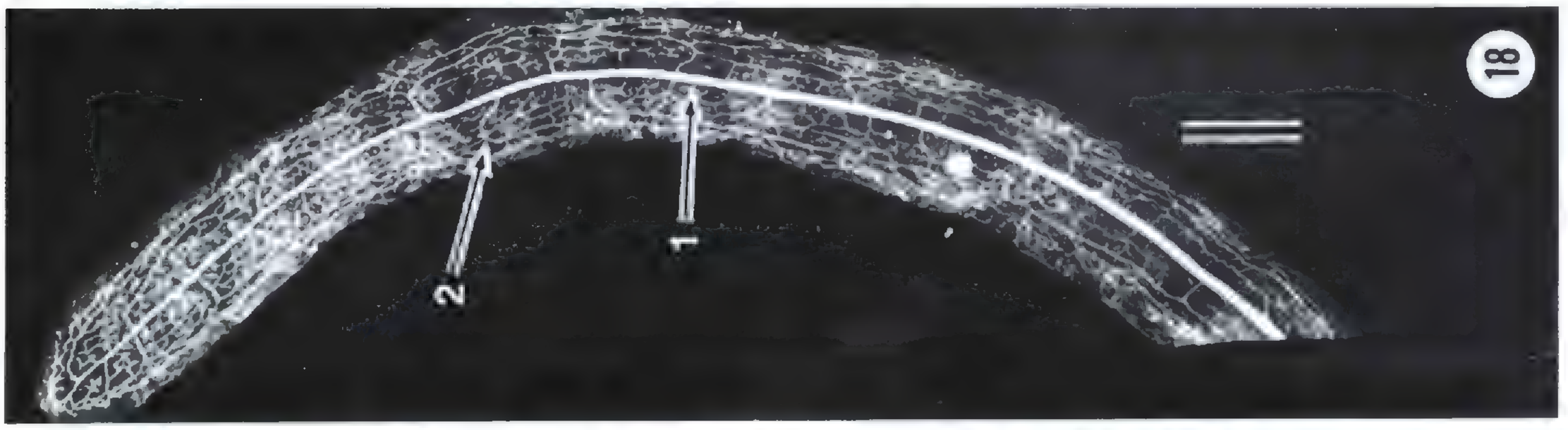
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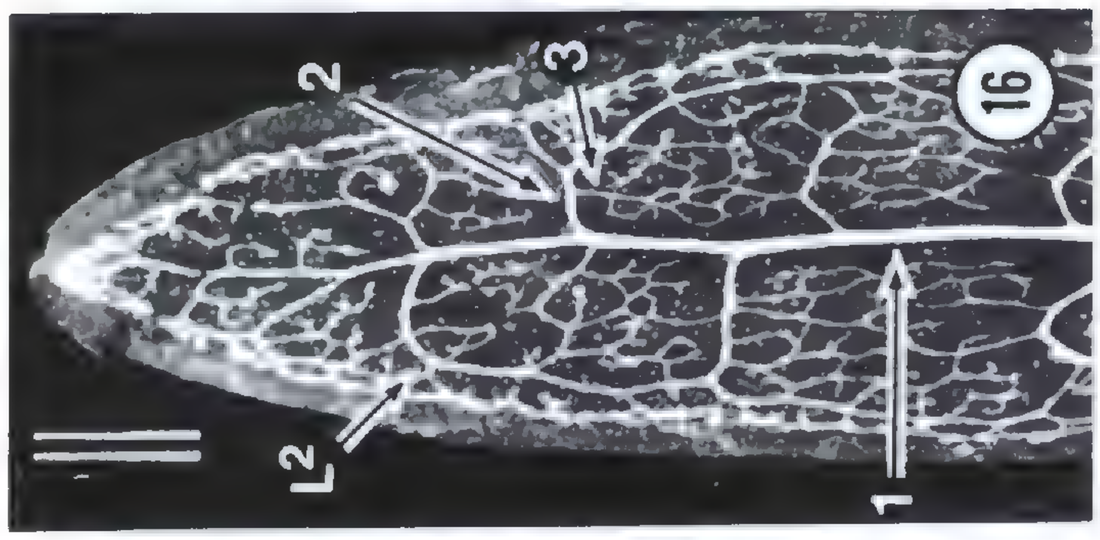
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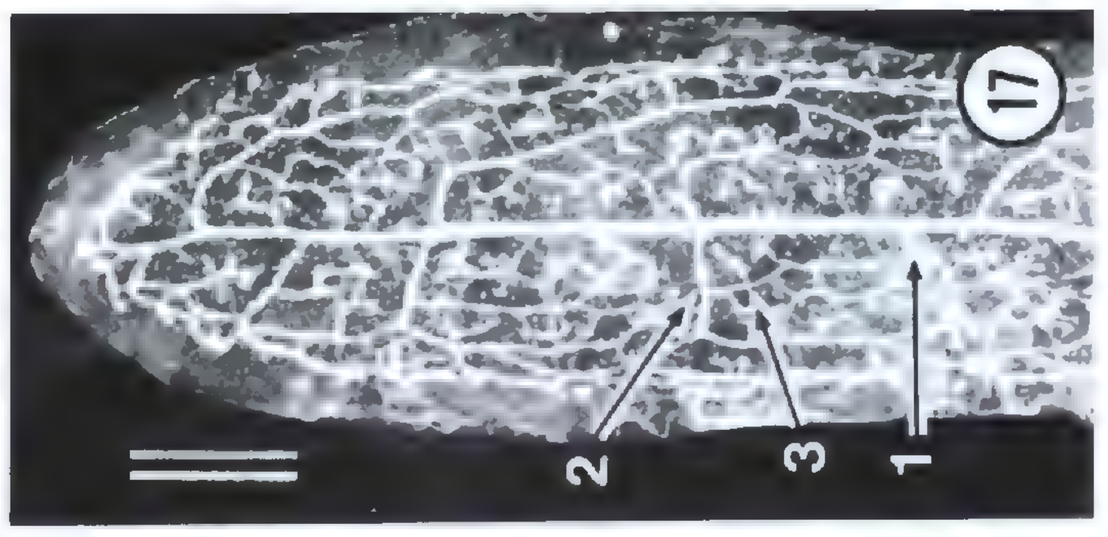
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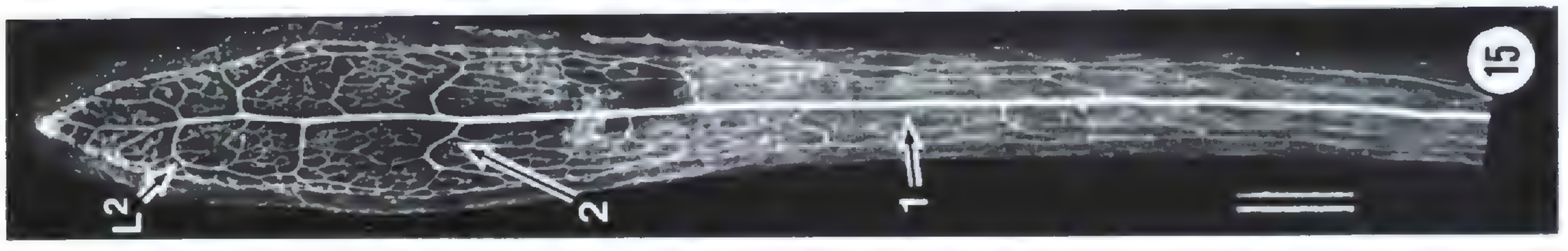
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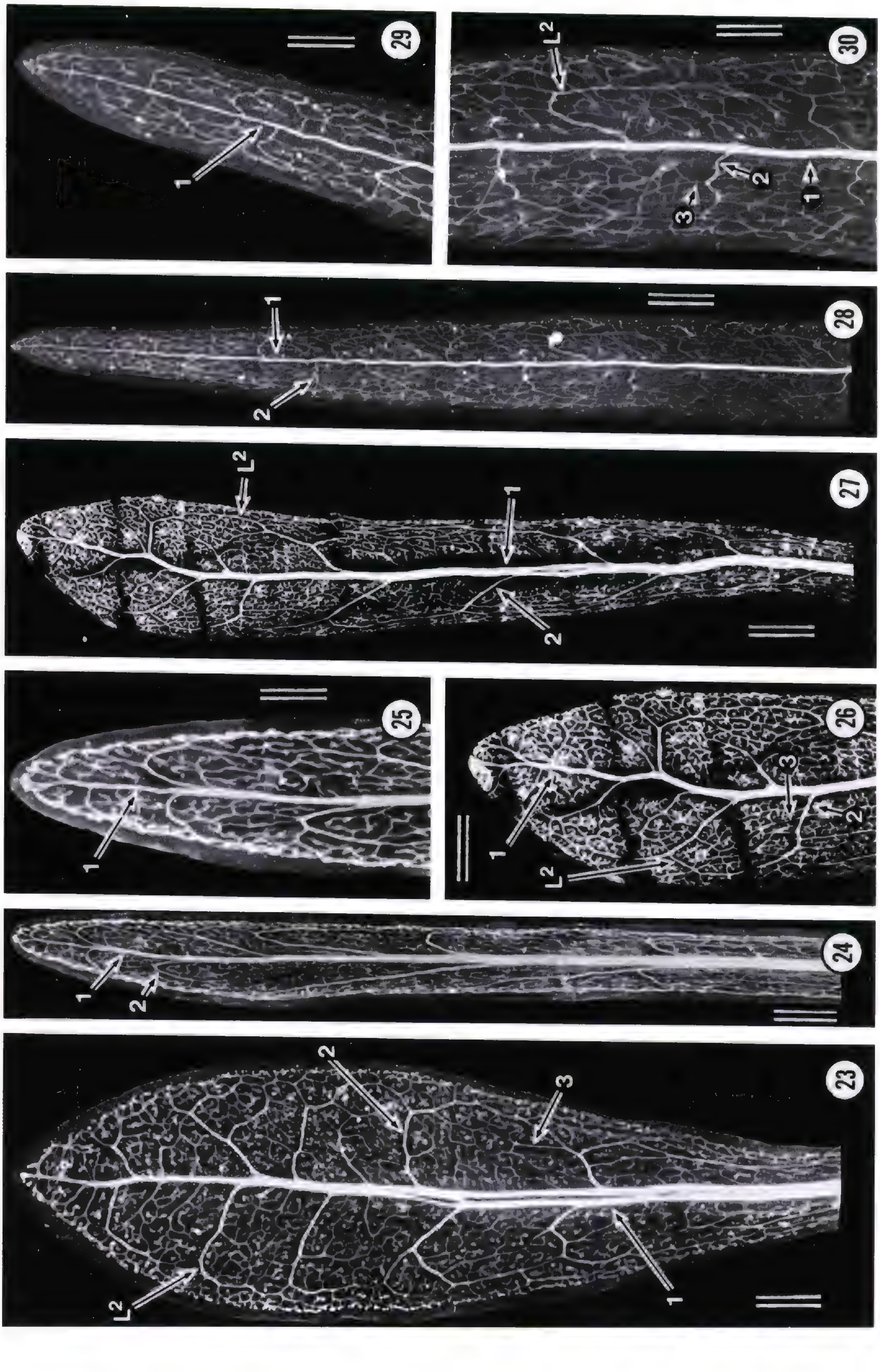
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irregular loops or recurve and ramify freely (Figs. 15–18). The higher-order venation in *C.* sect. *Acaules* (Figs. 7, 8, 10, 11, 13, 14, 16, 17, 35–37) is more open than in *C.* sects. *Calandrinia* and *Monocosmia*: the tertiary veins are more freely ramified; the areolation is less developed; more, and more highly branched, freely ending veinlets occur per ultimate vein-enclosure; and the marginal venation (in those taxa lacking a fimbrial vein) consists of irregular loops and freely ending veinlets. A fourth order of veins is sometimes distinct in larger leaves of *C.* sect. *Acaules* (Fig. 11).

The fimbrial vein in *C.* sects. *Calandrinia* and *Monocosmia* and species of *C.* sect. *Acaules* superficially resembles that found in Montieae, e.g., in *Montia parvifolia* (Figs. 31, 41). In Montieae, however, the fimbrial vein merges with the prominently dilated primary vein at the leaf apex and remains (or becomes) parallel to it; this morphology characterizes fimbrial veins in certain Caryophyllaceae (Hershkovitz, unpublished). The perpendicular orientation of the fimbrial vein at the leaf apex in *Calandrinia* is unique.

Venation in *Montiopsis* subgenera *Dianthoideae* (Figs. 19–25) and *Montiopsis* (Figs. 26–31) resembles that in species of *C.* sect. *Acaules* that lack fimbrial veins. The primary vein remains prominent and distinct at the leaf apex or becomes ramified at the extreme apex. The secondary veins may be irregularly ramified/reticulate (e.g., *M. andicola*, Fig. 22), ramified/recurved (e.g., *M. gayana*, Fig. 24), or form irregular loops (e.g., *M. gayana*, Fig. 23; *M. umbellata*, Figs. 26, 27; and *M. trifida*, Fig. 30). The tertiary veins form the highest distinct order and are irregularly ramified to reticulate.

Areolation is imperfect; the ultimate vein enclosures often have three or more, often branched, freely ending veinlets; and the marginal venation is finely looped to open. In some specimens of *M.* (*Dianthoideae*) *andicola*, a single veinlet protrudes into some of the larger basal leaf dentations (Fig. 19). The smallest leaves in these sections show little organization in venation pattern: one or two pairs of weakly distinct, ramified (rarely looped), secondary veins give rise to a few reticulating veins or freely ending veinlets.

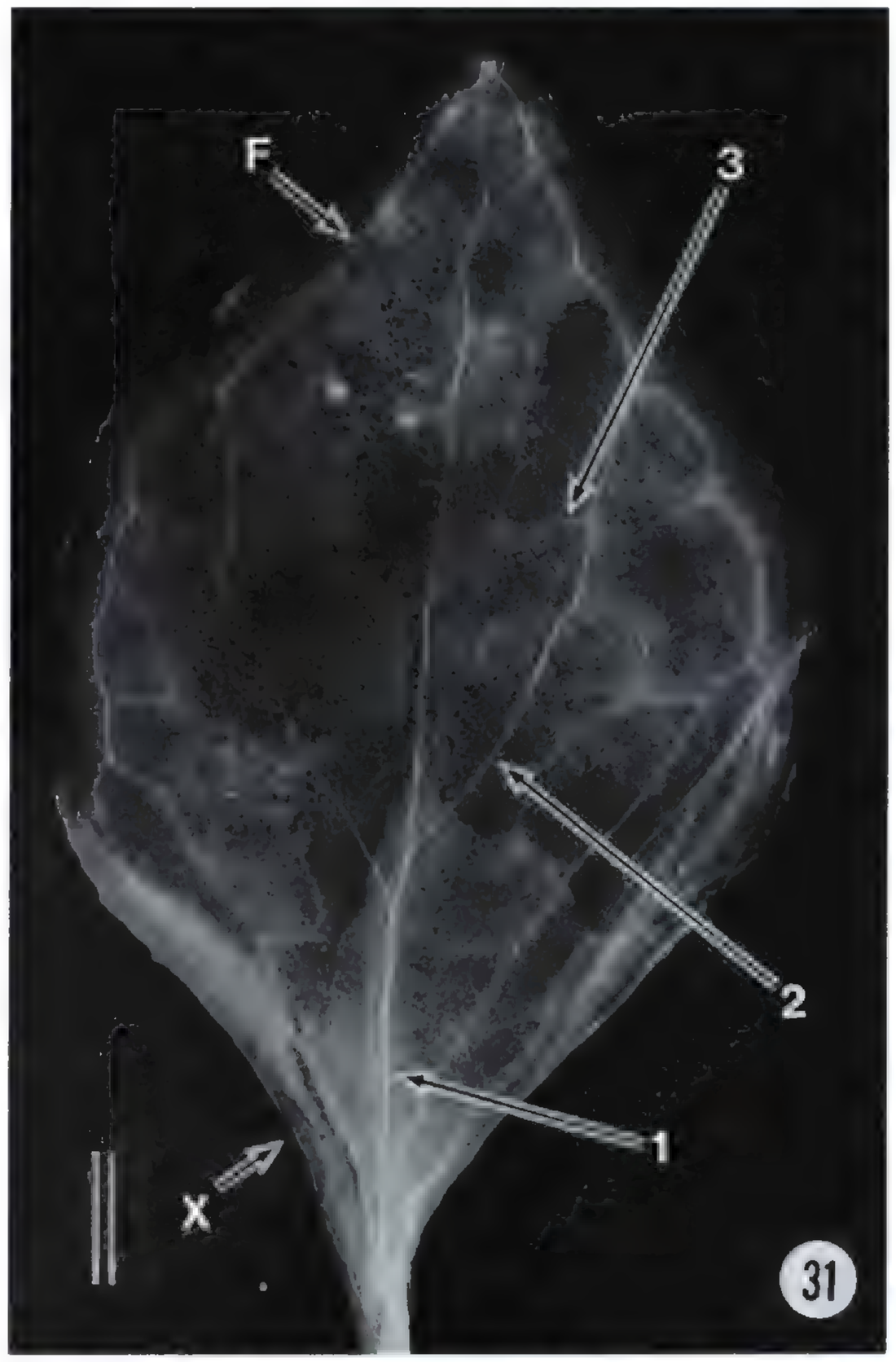


FIGURE 31.[3] Cleared leaf of *Montia parvifolia* (*Randall s.n.*). Voucher listed in Table 1. X, approximate position of the constriction between leaf blade and petiole. Scale bar = ca. 1.7 mm.

*3. Stomatal morphology.* Nyanyano (1986a, b) reported that, among the 22 species of *Calandrinia* sensu lato investigated, 15 had paracytic stomata and 7 had (presumably brachy-)tetracytic stomata. Nyanyano (1986a) did not identify the species of *Calandrinia* sensu lato examined other than the few he illustrated, so the correlation between his data and the taxonomic circumscriptions employed in the present paper cannot generally be ascertained. Nyanyano (1986a) did, however, illustrate brachytetracytic stomata in *C.* (*Acaules*) *acaulis* and also reported tetracytic stomata in *C.* (*Monocosmia*) *monandra*. He did not report variation in stomatal morphology within species, although variation in stomatal type is the rule in

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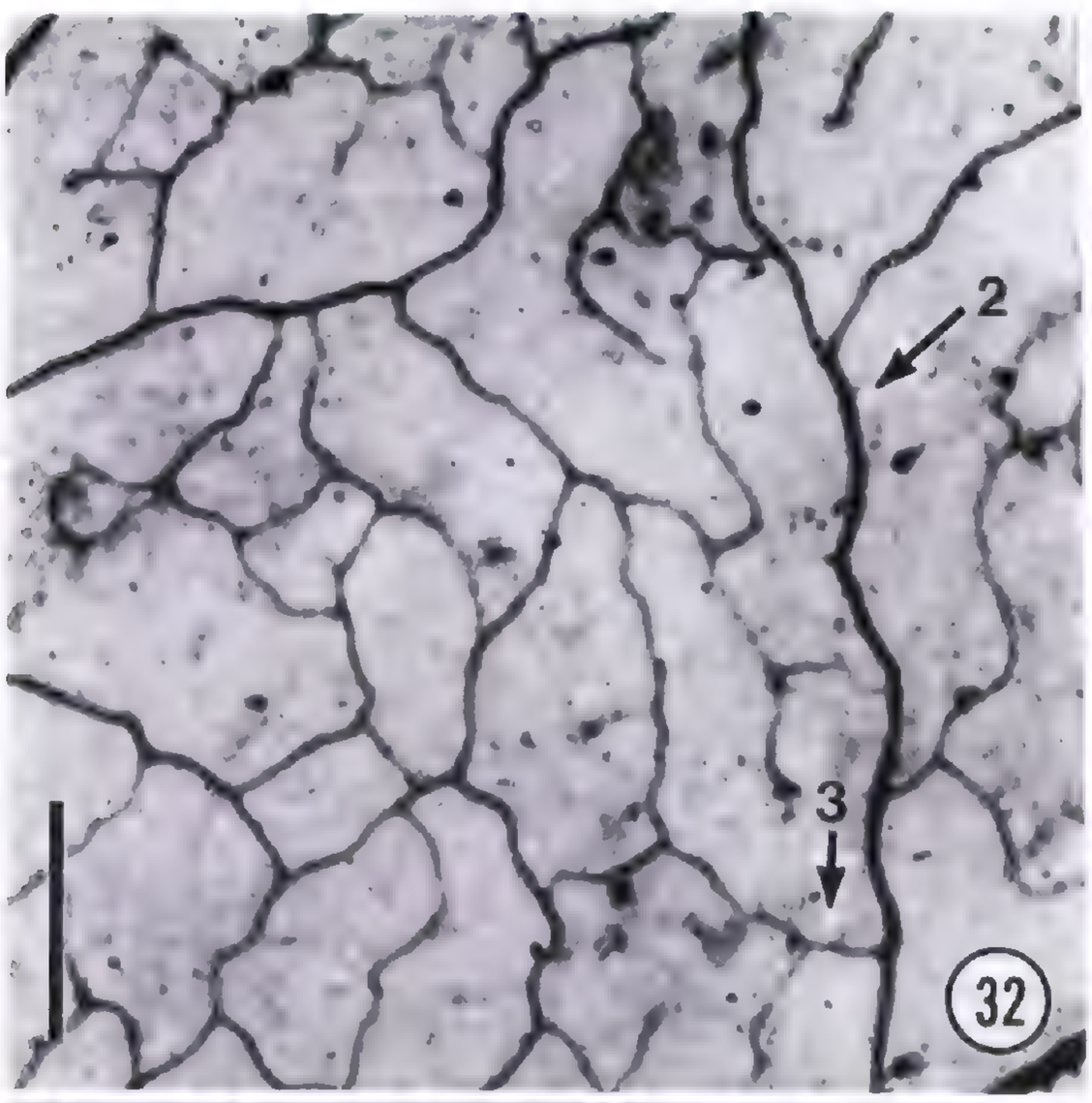
FIGURES 23–30.[3] Cleared leaves of *Montiopsis*. —23. Leaf blade of *M.* (*Dianthoideae*) *gayana* (*Buchtien 36*). 24, 25. *M. gayana* (*Joseph 3496*).—24. Leaf blade.—25. Leaf apex. 26, 27. *M.* (*Montiopsis*) *umbellata* (*Grau & Grau 1516*).—26. Leaf apex.—27. Leaf blade. 28–30. *M.* (*Montiopsis*) *trifida* (*Johnston 3592*).—28. Apical half of leaf blade.—29. Leaf apex.—30. Midlaminal portion. Scale bars are (mm) ca. 0.8, 1.3, 0.7, 0.8, 1.6, 1.1, 0.5, and 0.6, respectively.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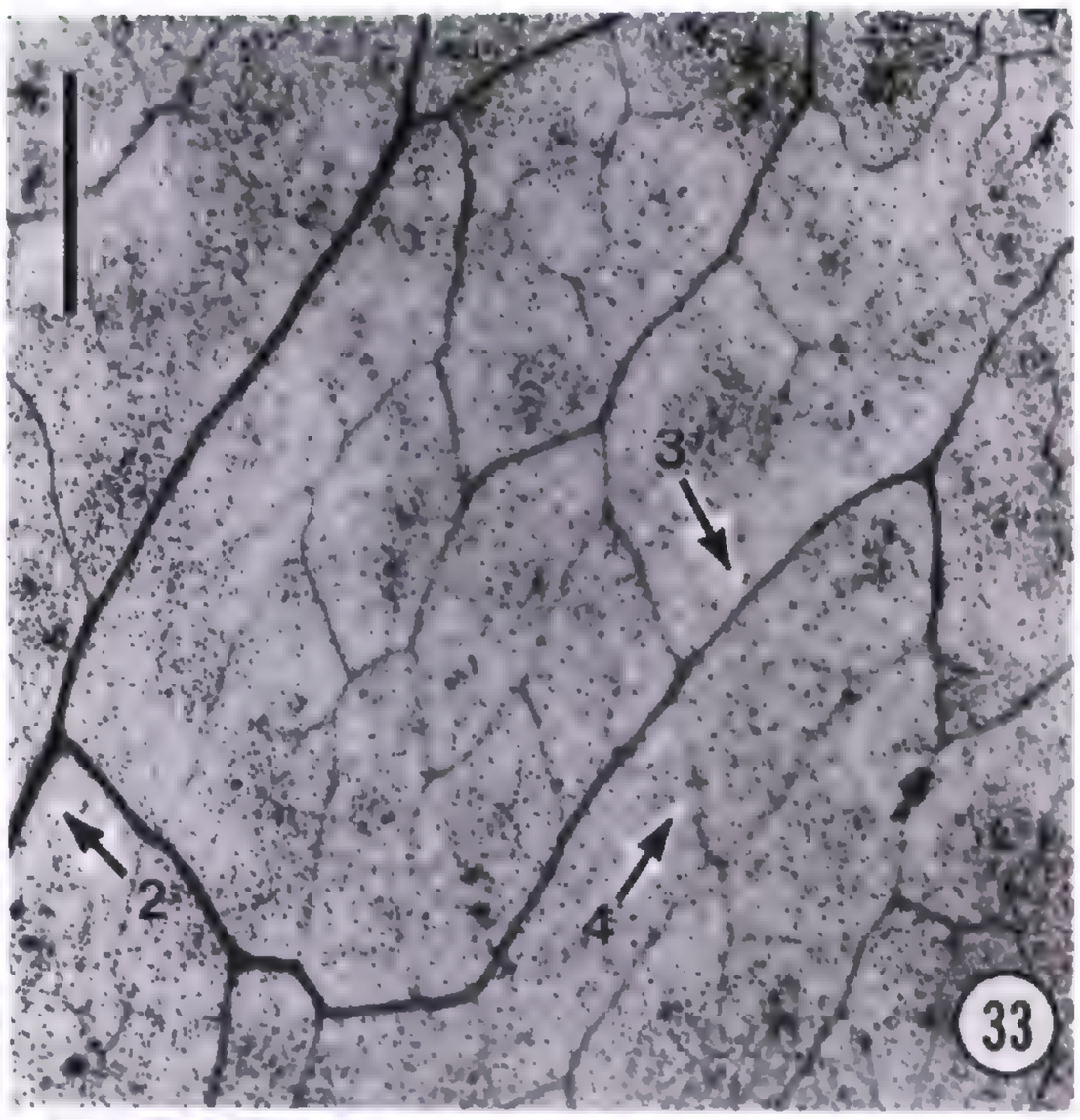
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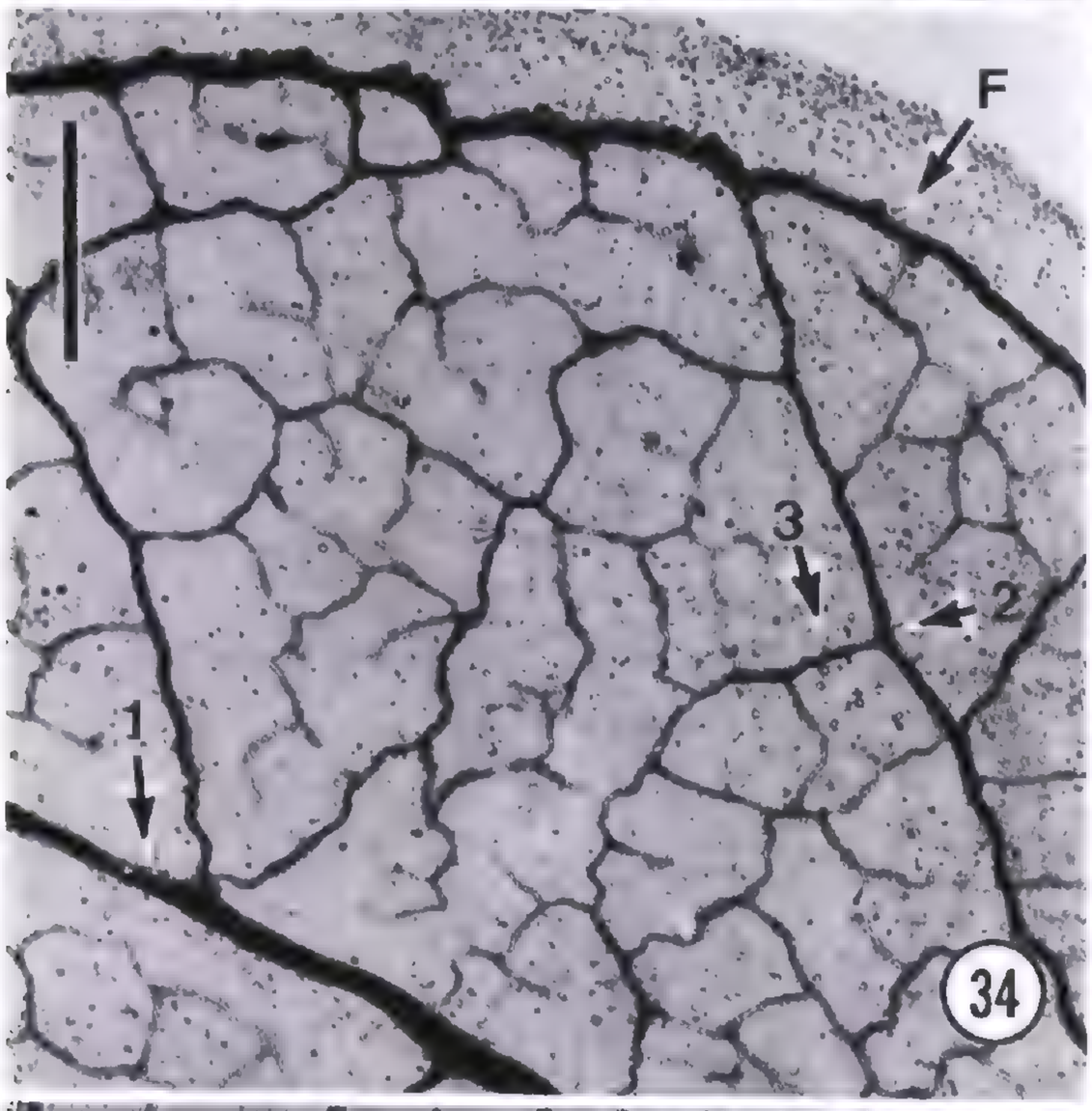
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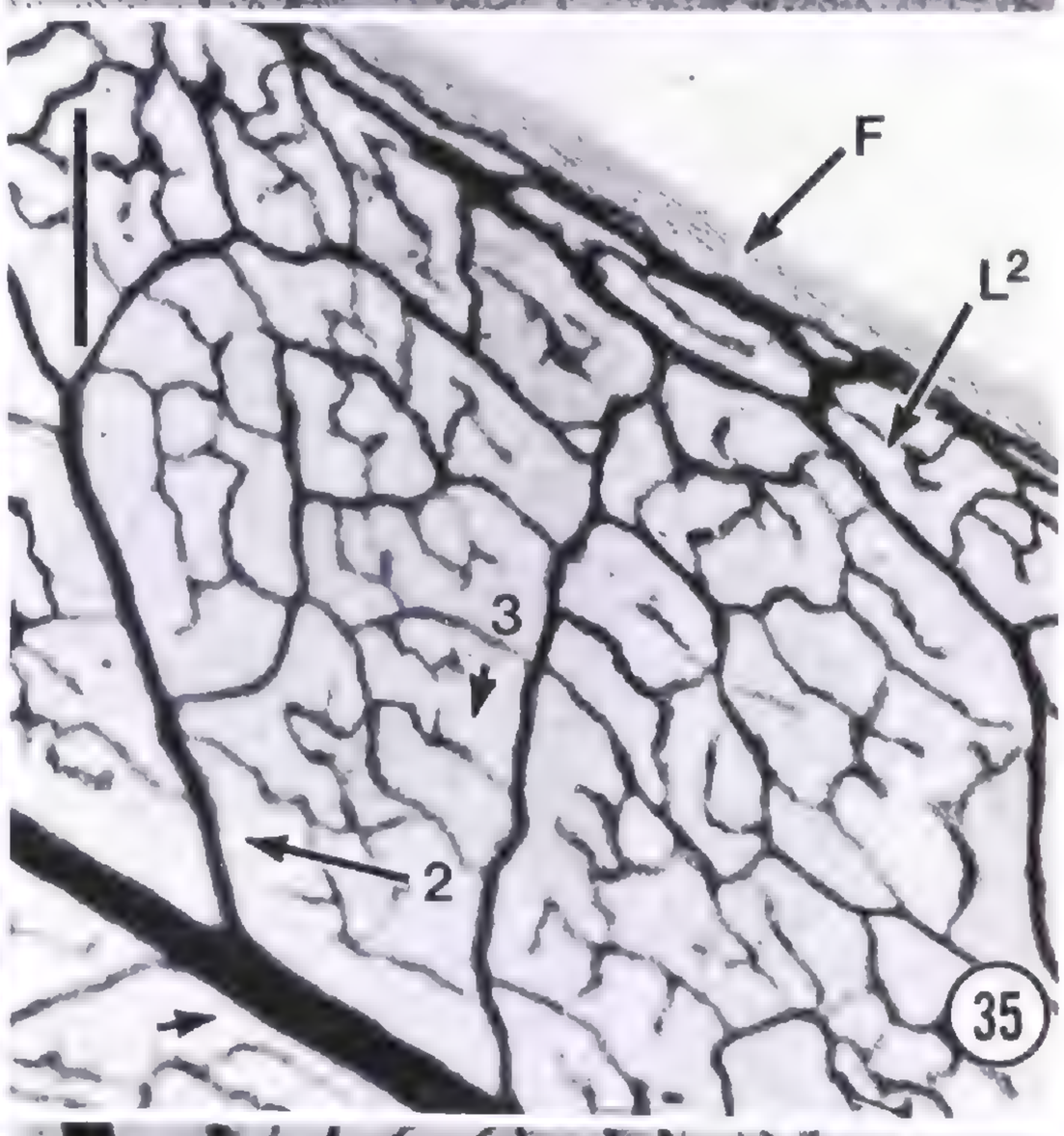
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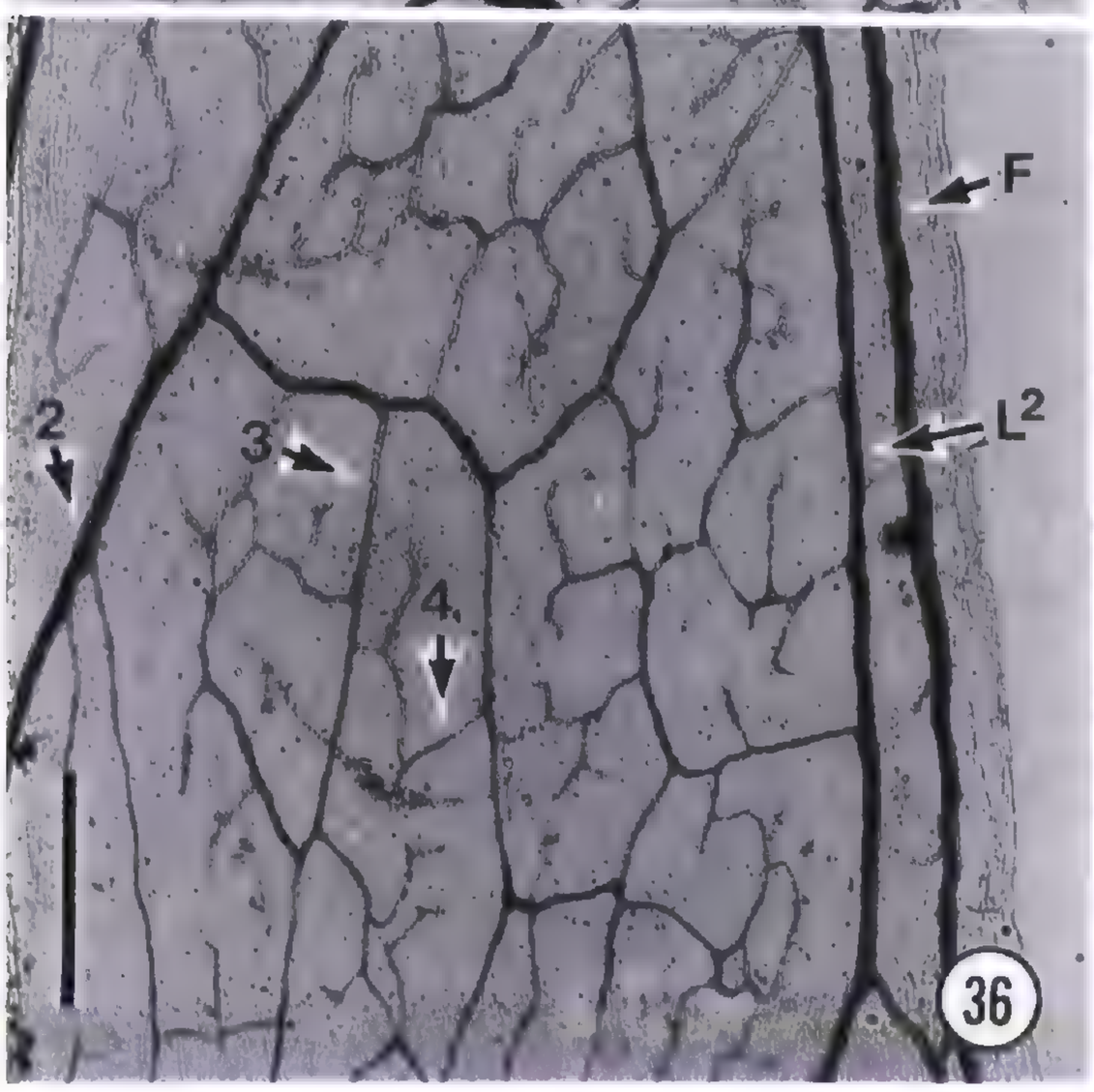
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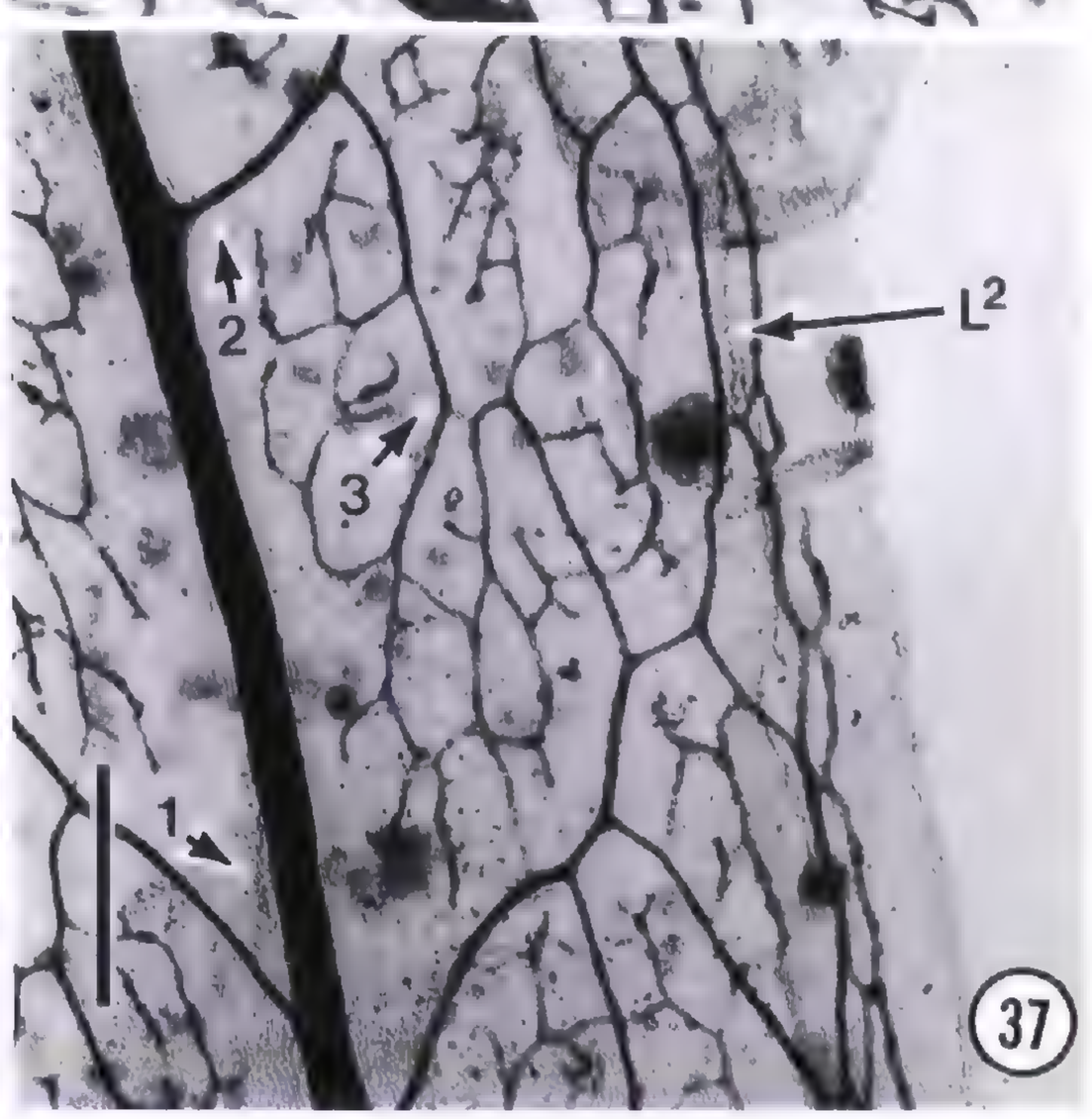
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individual leaves of *Calandrinia* and many other members of Portulacaceae (Hershkovitz, 1991a, 1992, unpublished).

Figures 42–54 illustrate stomatal morphology in species of *Calandrinia* and *Montiopsis*; for comparison, Figure 55 illustrates stomata of *Montia parvifolia*. I examined stomatal morphology in 33 specimens of ca. 25 species of *Calandrinia* and *Montiopsis*. For comparison, I examined stomata in selected taxa throughout Portulacaceae.

Stomata of *C.* sect. *Calandrinia*, including *C. alba* (Fig. 42), *C. breweri* (Fig. 43), and *C. axilliflora* (Fig. 44) are predominantly staurocytic (Figs. 42-1, -3, -4; 43-2; 44-1, -2) to brachytetracytic (Figs. 42-3, 43-1). The contact cells (i.e., the cells bordering the guard cells) are often surrounded by an additional cycle of "subsidiary-like" epidermal cells morphologically intermediate between subsidiary cells and ordinary epidermal cells (Fig. 42-2, -3). The inner tangential walls of these cells, which abut the subsidiary cells, form smooth arcs, but the outer tangential walls are generally more sinuous, like ordinary epidermal cells. Other stomatal types occur infrequently in *C.* sect. *Calandrinia*, including brachyparacytic, intermediates between brachyparacytic and brachytetracytic (e.g., brachyparacytic with one polar subsidiary cell, Fig. 44-3), hemi-amphibrachyparacytic (Fig. 43-3; cf. Hershkovitz, 1991a), amphibrachyhexacytic, anomocytic, and other minor morphological variants not readily classified. The number of contact cells in *C.* sect. *Calandrinia* is usually four or five.

*Calandrinia* (*Monocosmia*) *monandra* (Fig. 45) has stomatal morphology very similar to that of *C.* sect. *Calandrinia*.

Staurocytic and brachytetracytic stomata also occur commonly to predominantly in most of the examined taxa of *C.* sect. *Acaules*, including *C. carolinii* (Fig. 46), *C. colchaguensis* (Fig. 47), and *C. caespitosa* (Fig. 48). An outer cycle of subsidiary-like cells is also evident (Figs. 46-1; 47-2; 48-1, -2) but may be incomplete or poorly defined. Brachyparacytic and related stomatal types (e.g., amphibrachyparacytic, hemi-amphibrachyparacytic) appear to be more common in specimens of *C.* sect. *Acaules* (especially in *C. caespitosa*; Fig. 48) than in *C.* sects. *Calandrinia* and *Monocosmia*; such stomata predominate only in *C. compacta* (Fig. 49). Irrespective of stomatal type, the number of contact cells in *C.* sect. *Acaules* is usually four or five, rarely three or six.

The predominance of brachytetracytic and staurocytic stomata found in *C.* sects. *Calandrinia*, *Monocosmia*, and *Acaules* resembles the condition found in *Montia parvifolia* (Fig. 55). In this species, however, an outer cycle of cells is less discernable.

Brachy- to amphibrachyparacytic stomata predominate in *M.* subg. *Dianthoideae*, e.g., in *M. gayana* (Fig. 50) and *M. andicola* (Fig. 51). Staurocytic stomata sometimes occur commonly but never predominantly (e.g., *M. gayana*, Fig. 50). These staurocytic stomata are often surrounded by an irregular outer cycle of subsidiary-like cells similar to that found in *Calandrinia*. The number of contact cells in *M.* subg. *Dianthoideae* is most commonly four or five.

Brachy- to amphibrachyparacytic stomata also predominate in *M.* subg. *Montiopsis*, e.g., in *M. copiapina* (Fig. 52), *M. gilliesii* (Fig. 53), *M. capitata*, and *M. umbellata*. Staurocytic stomata occur infrequently in *M. copiapina*, and an outer cycle of subsidiary-like cells is sometimes distinguishable. Hemibrachyparacytic and anomocytic stomata predominate in *M. parviflora* (Fig. 54). The number of contact cells in *M.* subg. *Montiopsis* is usually four but may be as many as six (Fig. 54).

*4. Trichome morphology.* Kelley (1973) reported unicellular ribbed trichomes in all species of *C.* sect. *Calandrinia*; no trichomes in *C.* sect. *Acaules*; glandular or eglandular, unbranched or branched multiseriate-multicellular trichomes in all species of *Montiopsis*; and, additionally, barbellate multiseriate-multicellular trichomes in all species of *Montiopsis* subg. *Montiopsis*. Carolin (1987) scored *C.* sects. *Calandrinia* and *Monocosmia* for having simple trichomes, the OTUs of *Montiopsis* for having both multicellular and glandular trichomes, and *C.* sect. *Acaules* for having glandular trichomes (but neither unicellular nor multicellular trichomes). Peralta's (1988) descriptions of trichomes in Mendozan species of *Montiopsis* accord

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FIGURES 32–37.[3] Higher order venation in *Calandrinia*.—*32. C.* (*Calandrinia*) *axilliflora* (*Joseph 2786*).—33. *C.* (*Calandrinia*) *breweri* (*Hoover 6697*).—34. *C.* (*Monocosmia*) *monandra* (*Buchtien 37*).—35. *C.* (*Acaules*) *affinis* (*Werdermann 606*).—36. *C.* (*Acaules*) *acaulis* var. *magna* (*Killip & Smith 21648*).—37. *C.* (*Acaules*) *carolinii* (*Venturi 4824*). All scale bars = ca. 500 μm.

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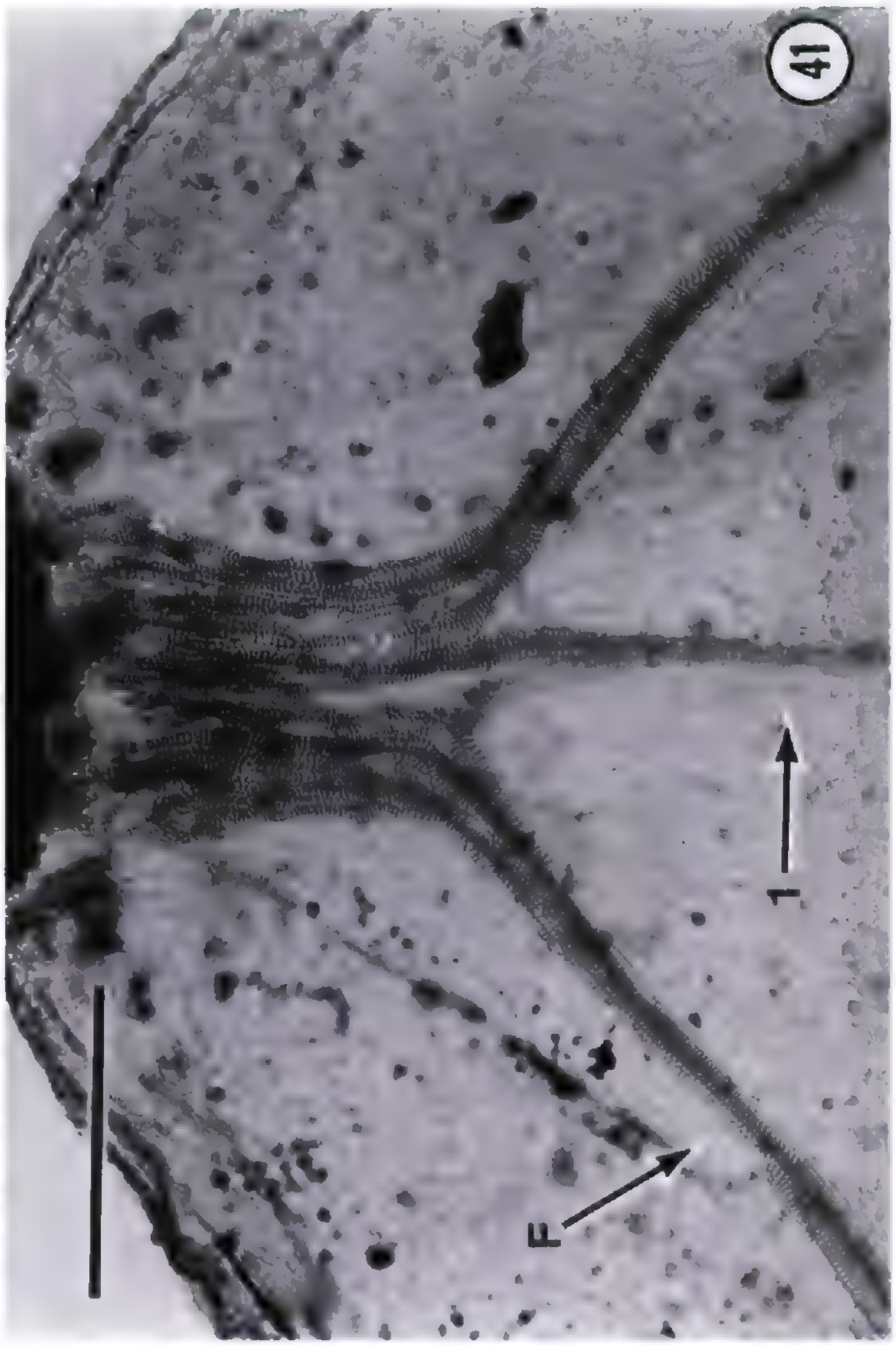
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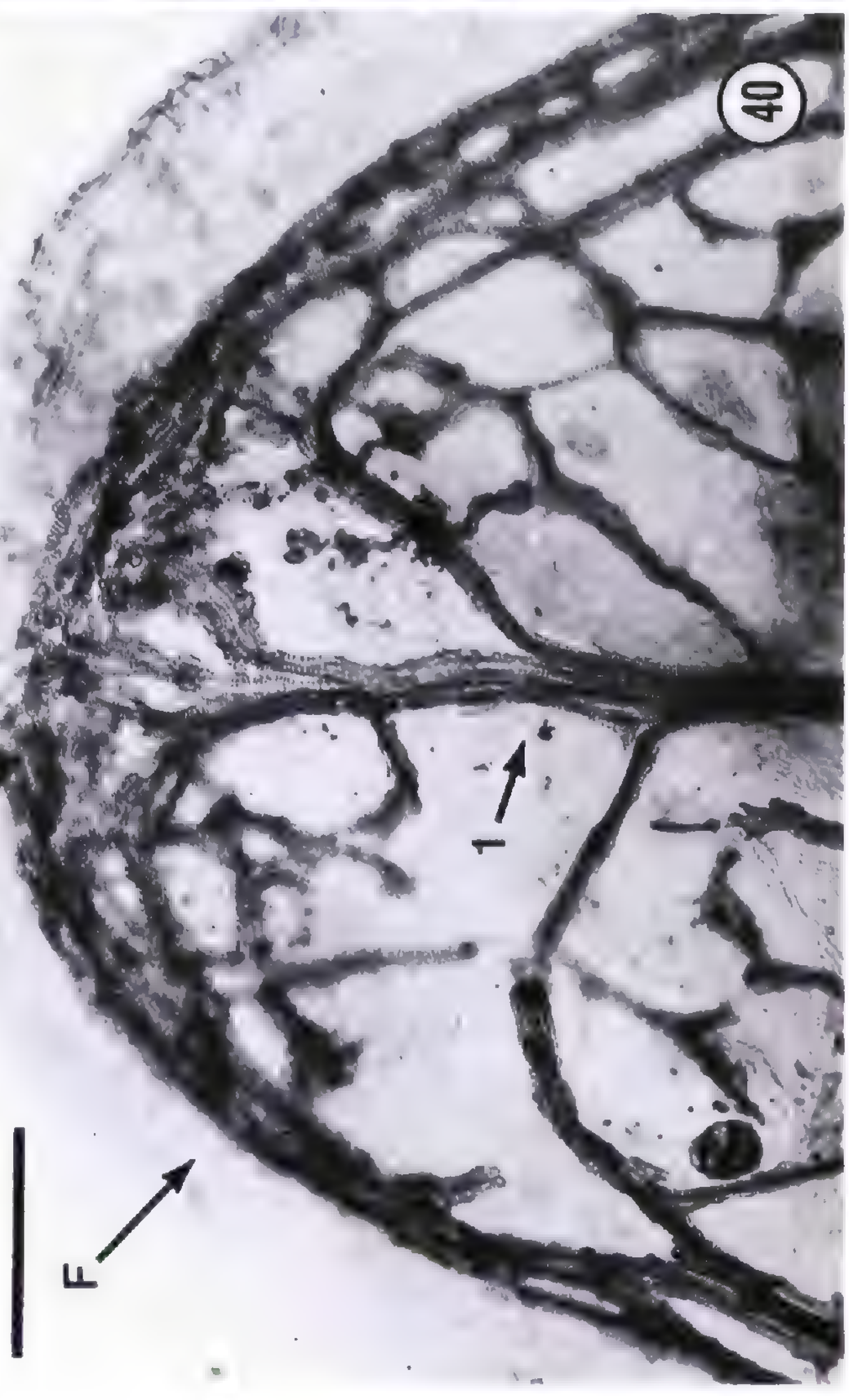
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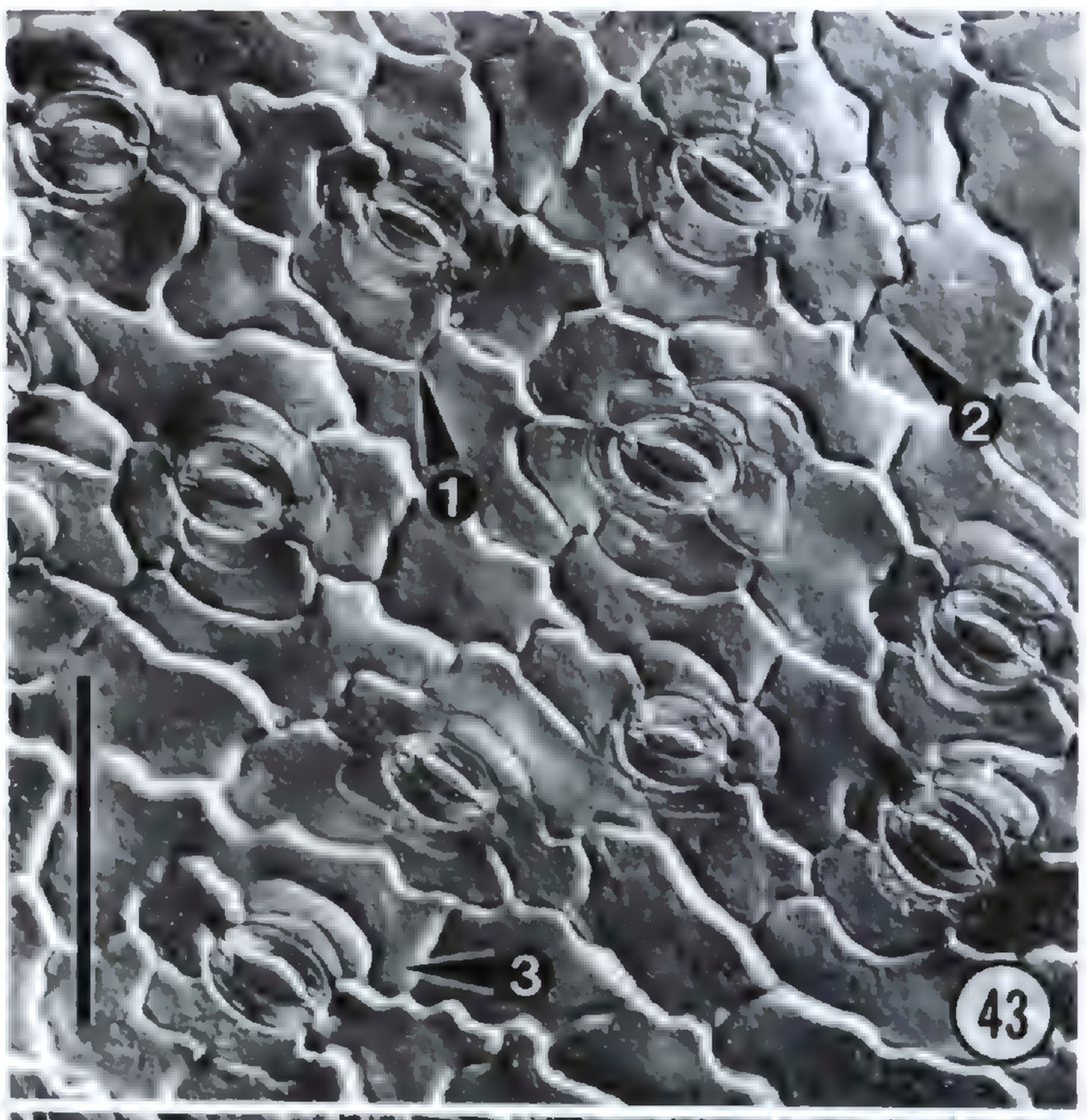
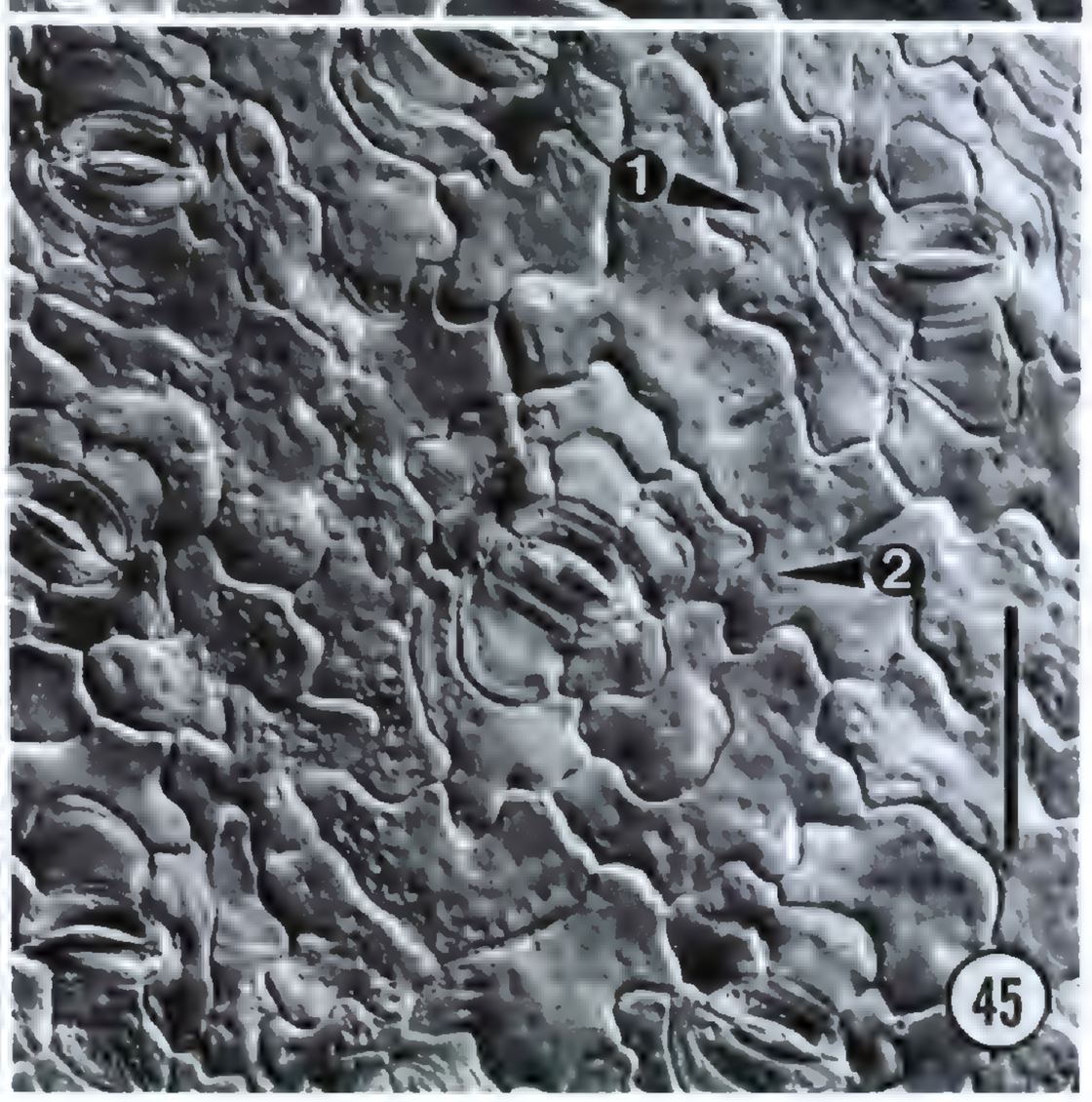


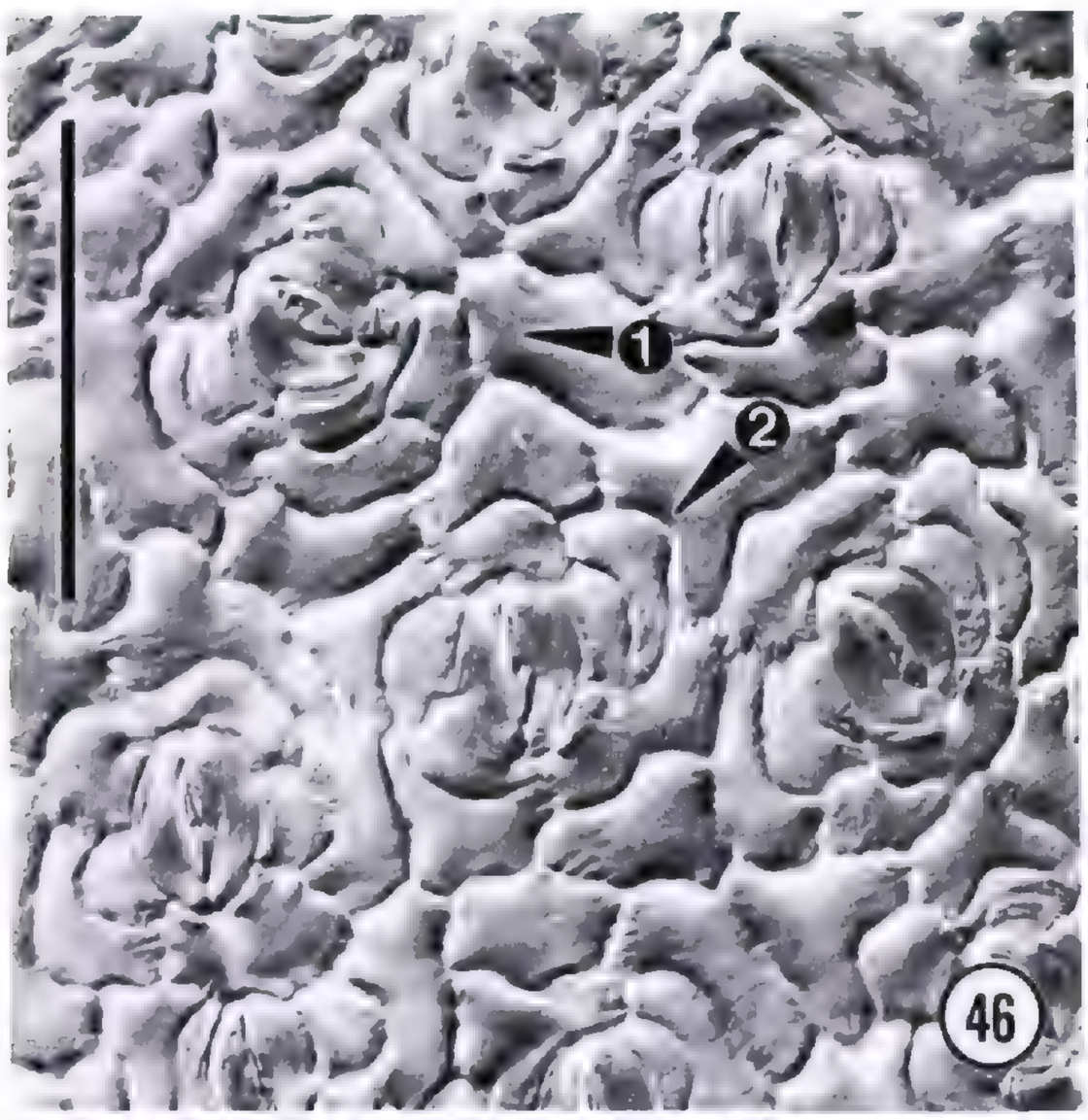


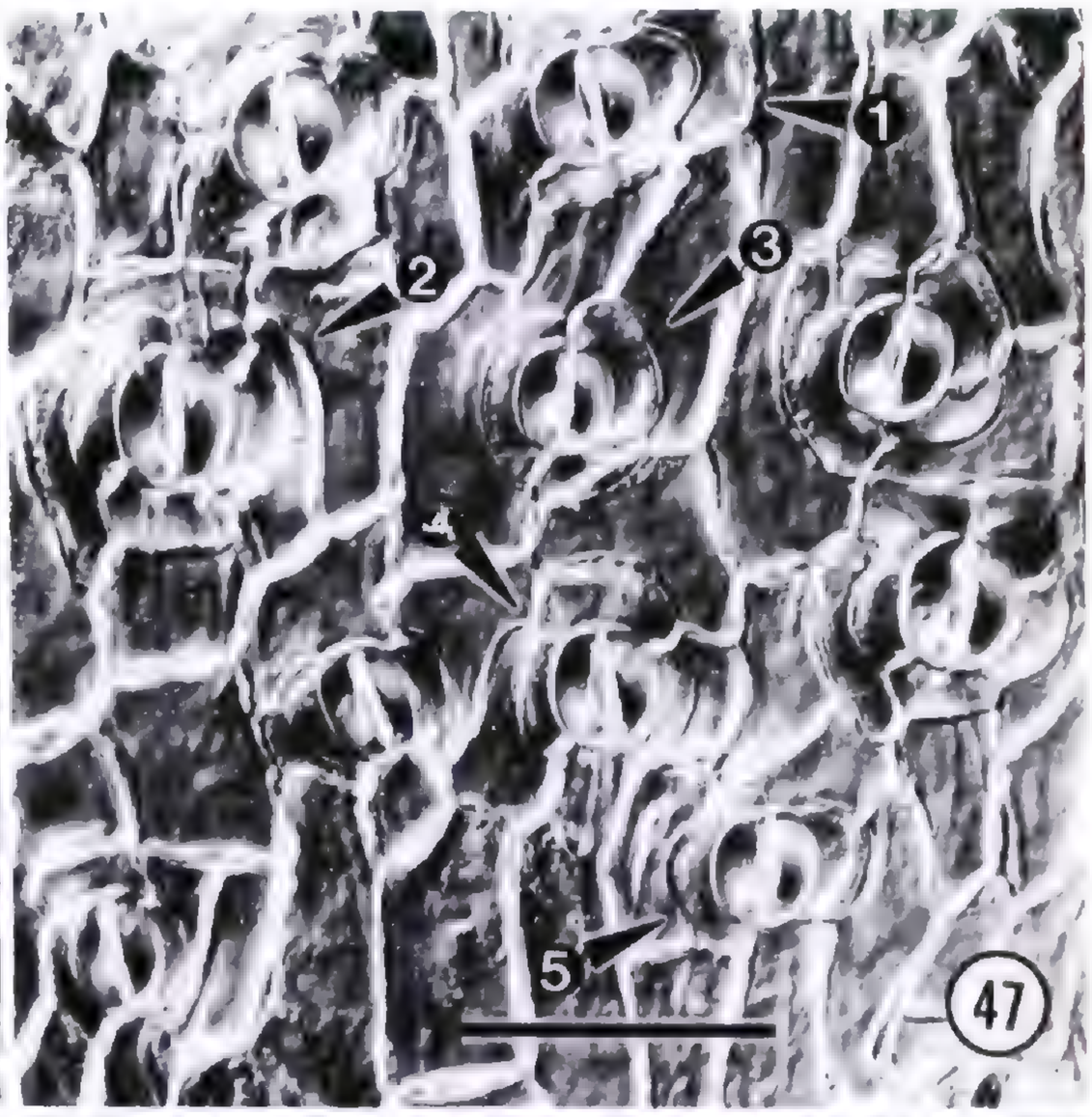

FIGURES 42–45.[1] Epidermal preparations of *Calandrinia* sects. *Calandrinia* and *Monocosmia*.—42. *C.* (*Calandrinia*) *alba* (*Lopez 1223*). 1, stauro-; three contact cells; outer cycle of three cells. 2, brachytetra-; outer cycle of cells. 3, stauro-; four contact cells; partial outer cycle of cells. 43. *C.* (*Calandrinia*) *breweri* (*Hoover 6697*). 1, brachytetra-; without distinct cycle of outer cells. 2, stauro-; five contact cells; weakly differentiated outer cycle of five cells. 3, more or less hemi-amphibrachypara-.—44. *C.* (*Calandrinia*) *axilliflora* (*Joseph 2786*). 1, stauro-; three contact cells; partial outer cycle of cells. 2, stauro-; four contact cells; partial outer cycle of cells. 3, brachypara-; one polar subsidiary cell; without distinct outer cycle of cells.—45. *C.* (*Monocosmia*) *monandra* (*Joseph 3719*). 1, brachytetra-; without distinct cycle of outer cells. 2, stauro-; five contact cells and nearly enclosing outer cycle of five cells. Scale bars are (μm) ca. 100, 100, 100, and 50, respectively.

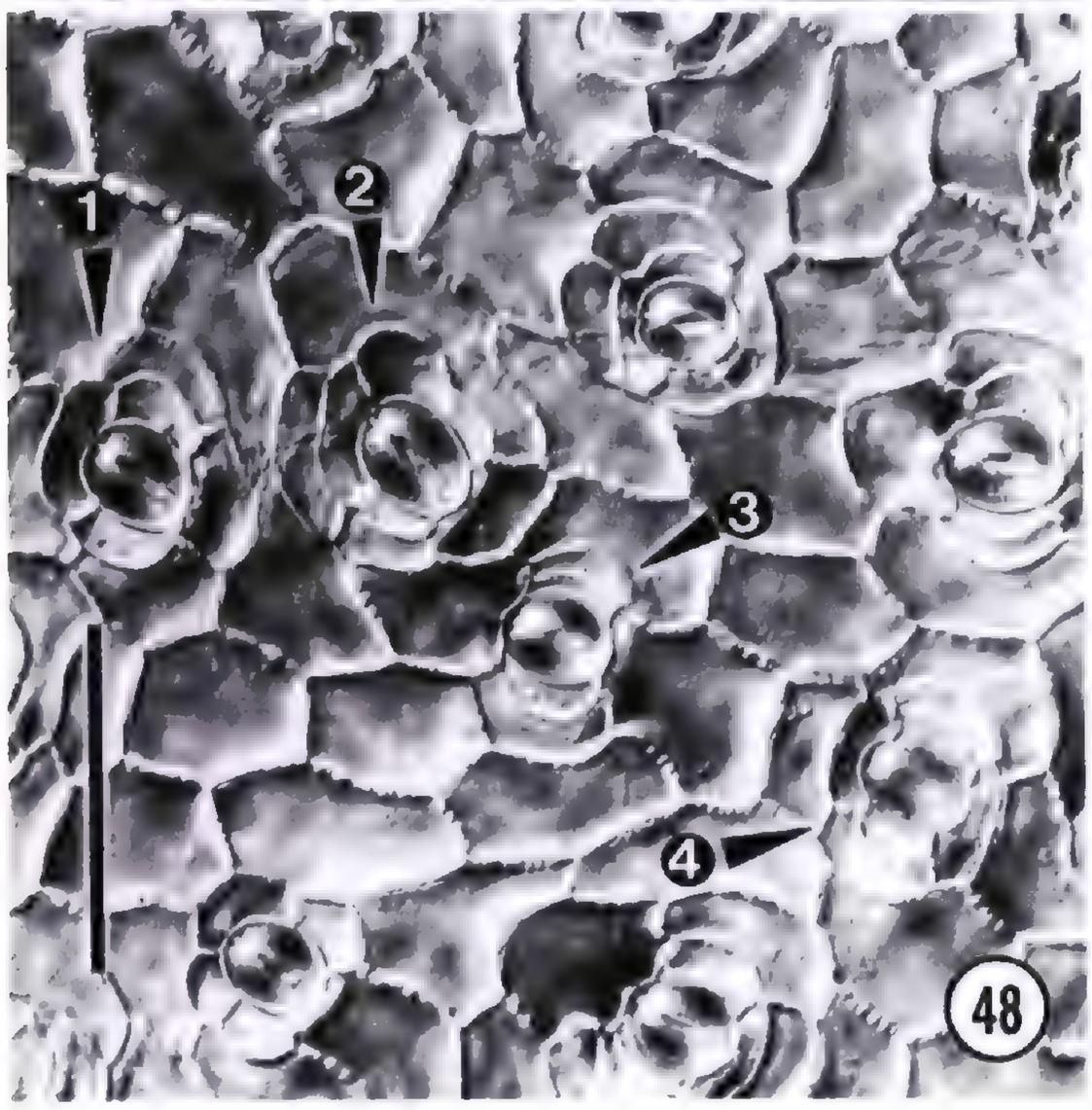
[1] FIGURES 42–69. Epidermal preparations of *Calandrinia*, *Montiopsis*, *Montia*, and *Rumicastrum*. The suffix -cytic is omitted from stomatal types. Specimens are vouchered, Table 1.

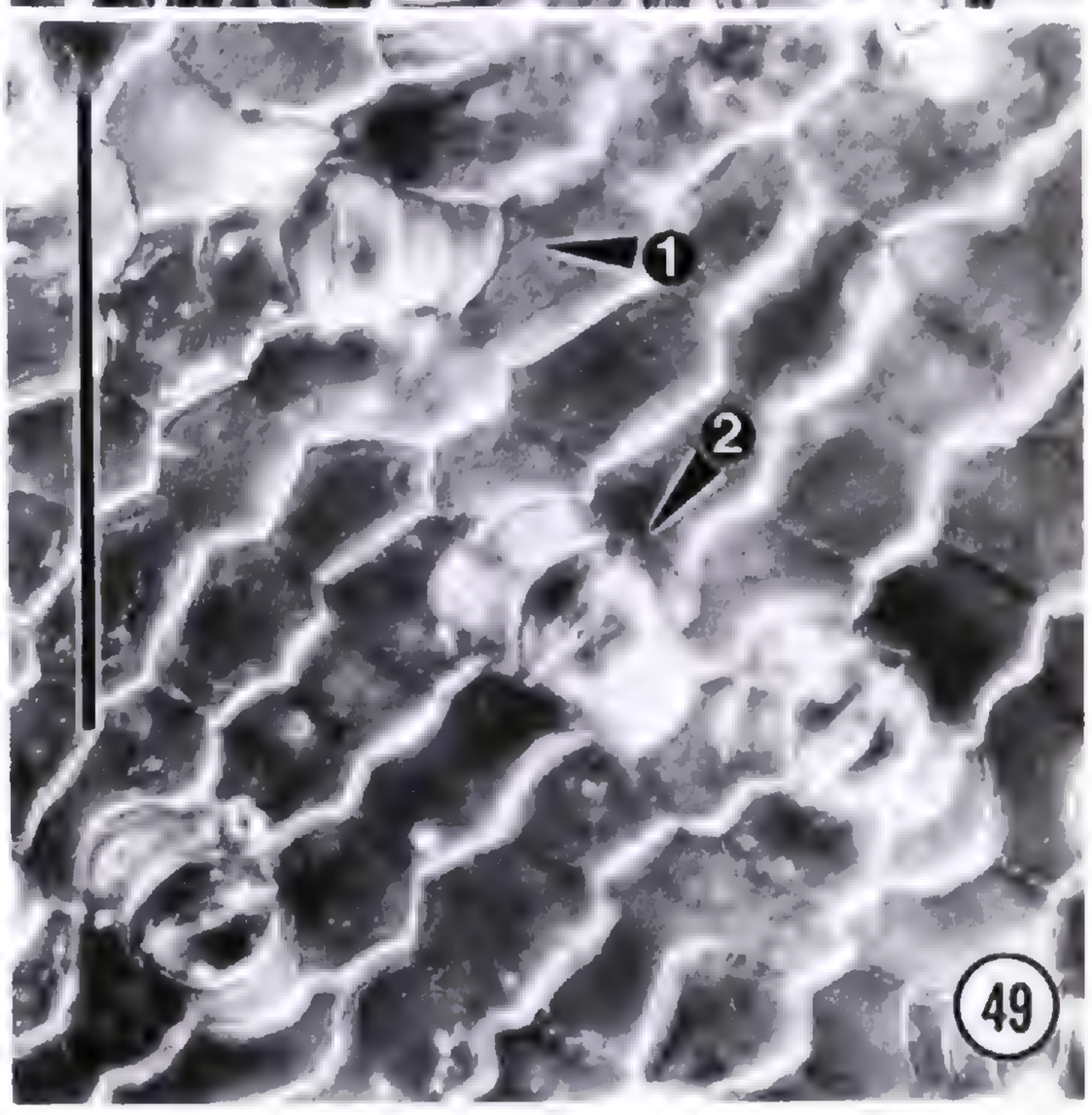
←

FIGURES 38–41. Cleared leaf apices of *Calandrinia* and *Montia parvifolia*. 1, primary vein; F, fimbrial vein. -38. *Calandrinia* (*Calandrinia*) *axilliflora* (*Joseph 2786*). 39. *Calandrinia* (*Monocosmia*) *monandra* (*Buchtien 37*).—40. *Calandrinia carolinii* (*Venturi 4824*).—41. *Montia parvifolia* (*Randall s.n.*). All scale bars = ca. 200 μm.



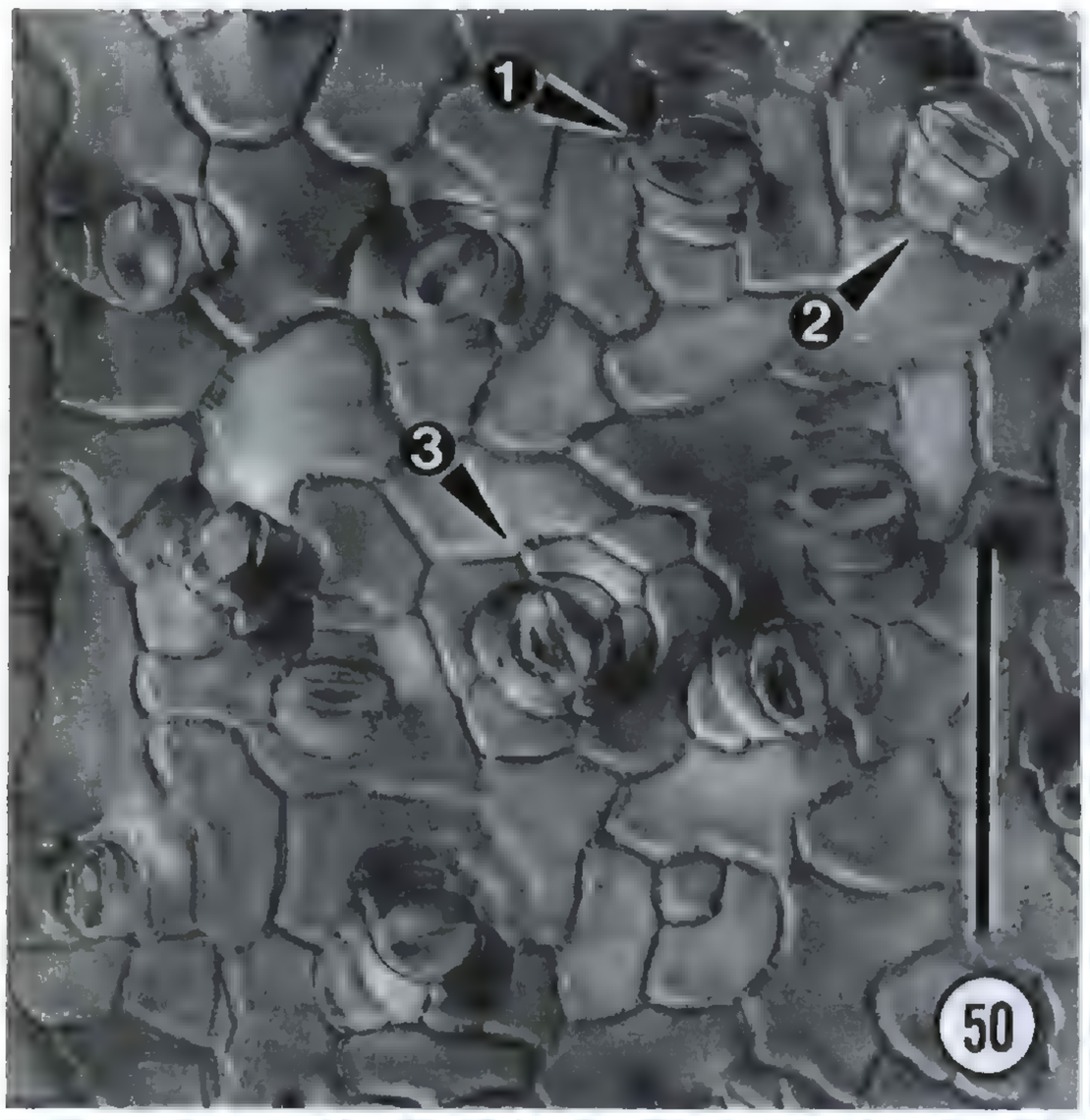




FIGURES 46–49.[3] Epidermal preparations of *Calandrinia* sect. *Acaules*.—46. *C. carolinii* (*Venturi 8786*). 1, brachytetra-; partial outer cycle of cells. 2, stauro-; three contact cells and weak evidence of outer cycle of cells.—47. *C. colchaguensis* (*Werdermann 1325*). 1, brachytetra-; without a distinct outer cycle of cells. 2, irregularly brachytetra-; outer cycle of cells. 3, stauro-; three contact cells; without outer cycle of cells. 4, more or less hemi-amphibrachypara-; one polar subsidiary cell. 5, brachypara-.—48. *C. caespitosa* (*Schjovskoy s.n.*). 1, brachytetra-; weak evidence of outer cycle of cells. 2, stauro-; five contact cells; partial outer cycle of cells. 3, amphibrachypara-. 4, hexa-.—49. *C. compacta* (*Werdermann 1035*). 1, hemi-amphibrachypara-. 2, essentially brachypara-; two subsidiary cells adjacent to one of the guard cells. All scale bars = ca. 100 μm.

→

FIGURES 50–55.[4] Epidermal preparations of *Montiopsis* and *Montia parvifolia*.—50. *Montiopsis* (*Dianthoideae*) *gayana* (*Werdermann 1219*). 1, amphibrachypara-. 2, hemi-amphibrachypara-. 3, stauro-; four contact cells; nearly complete outer cycle of cells.—51. *Montiopsis* (*Dianthoideae*) *andicola* (*Hastings 488*). 1, hemi-amphibrachypara-. 2, brachypara-.—52. *Montiopsis* (*Montiopsis*) *copiapina* (*Johnston 6069*). 1, amphibrachypara-. 2, stauro-; four contact cells; weak evidence of an outer cycle of cells. 53. *Montiopsis* (*Montiopsis*) *gilliesii* (*Buchtien 1149*). 1, hemi-amphibrachypara-. 2, amphibrachypara-.—54. *Montiopsis* (*Montiopsis*) *parviflora* (*Johnston 5882*). 1, anomo-; four contact cells. 2, anomo-; six contact cells. 3, anomo-; five contact cells. 4, hemibrachypara-.—55. *Montia parvifolia* (*Calder et al. 14865*). 1, stauro-; four contact cells. 2, brachytetra-. 3, stauro-; three contact cells. All scale bars = ca. 100 μm.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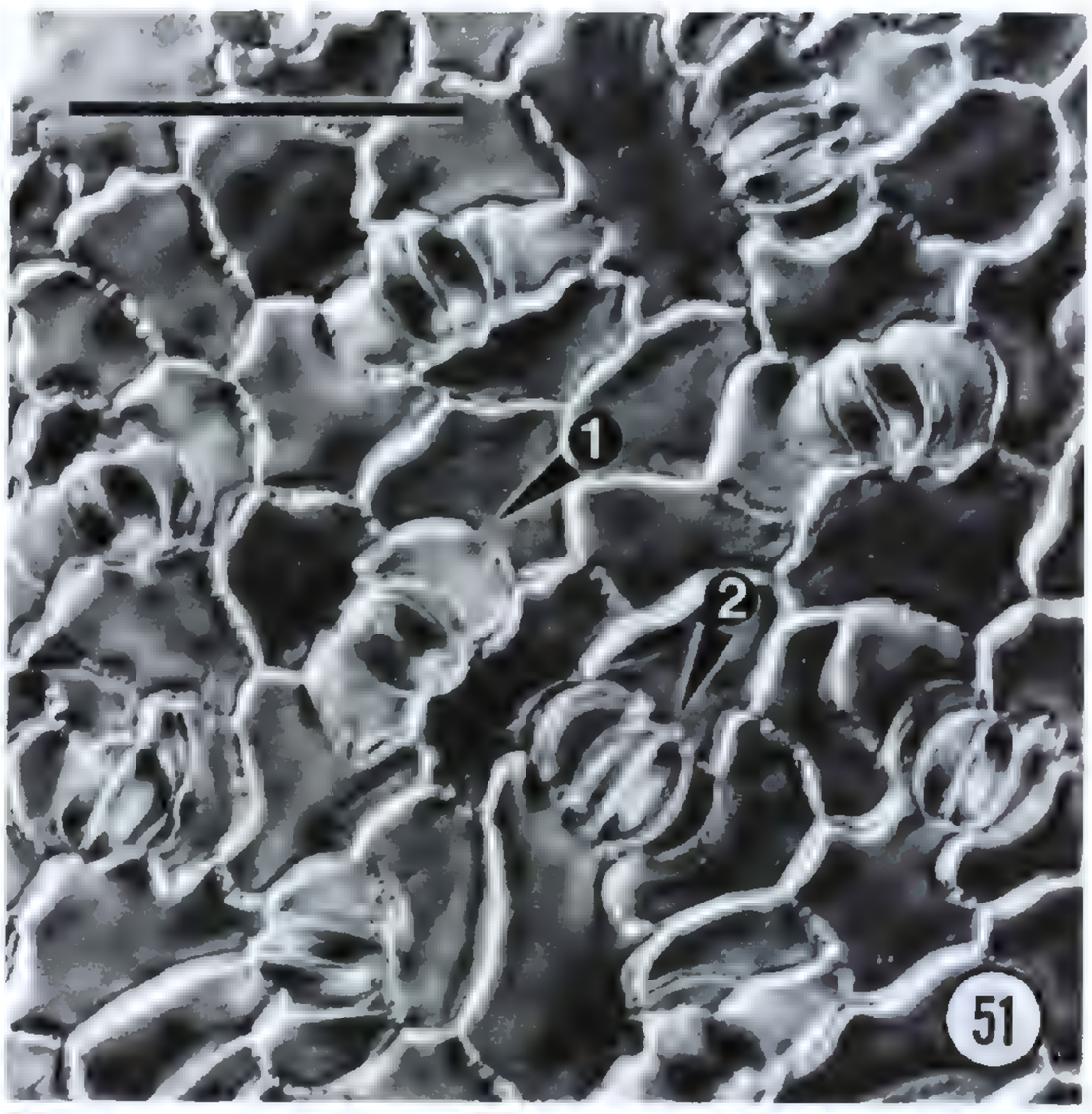
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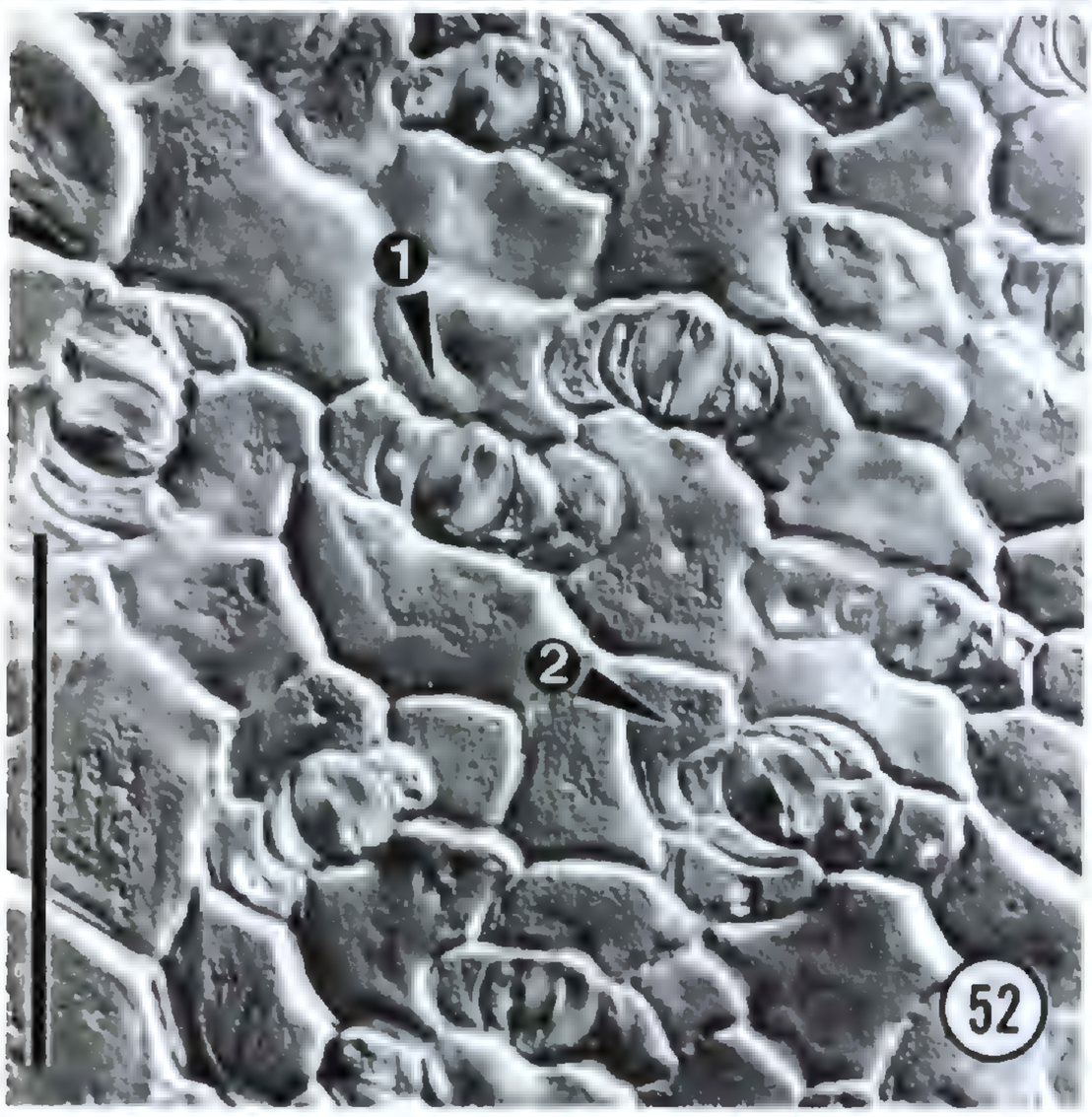
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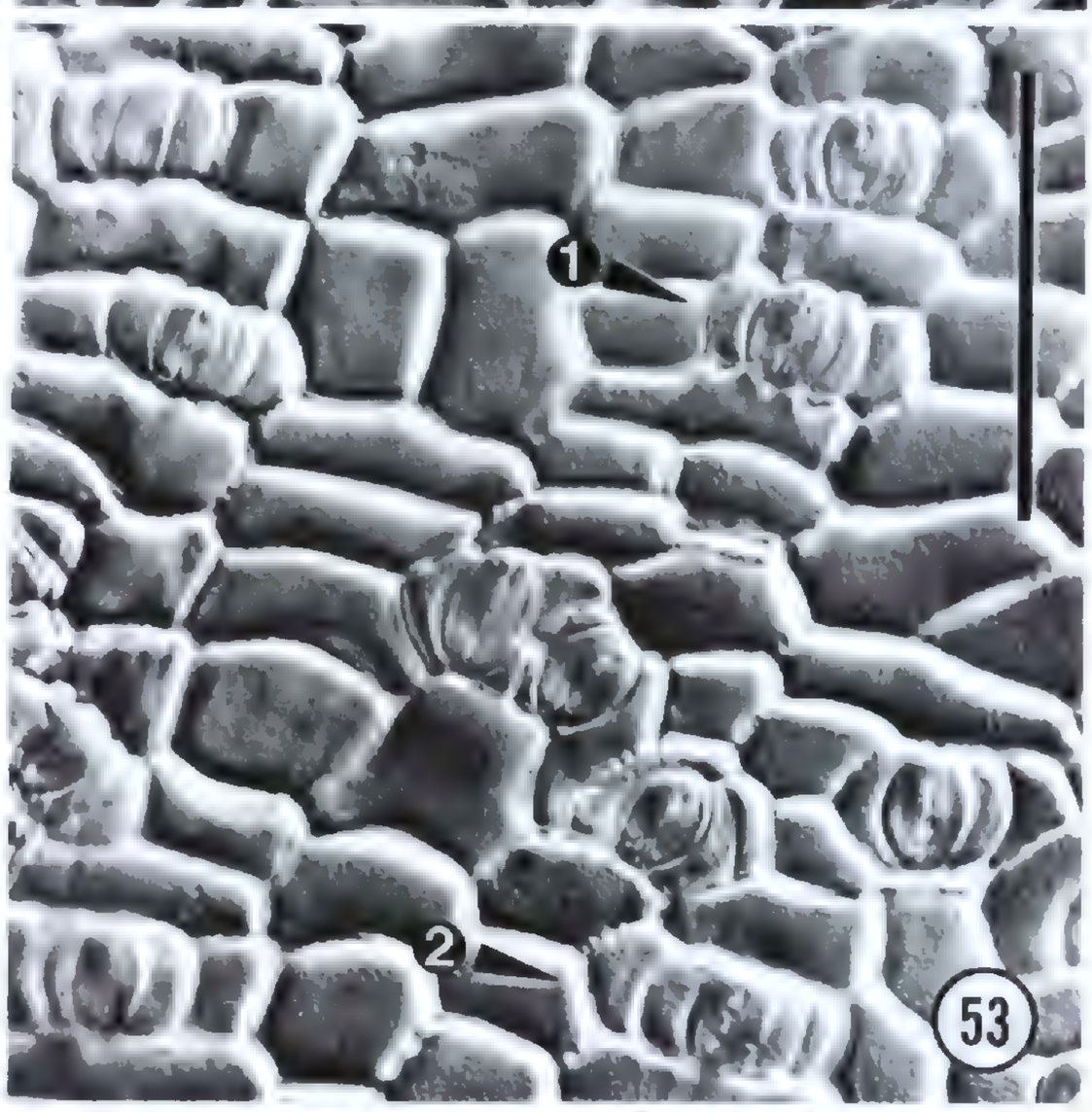
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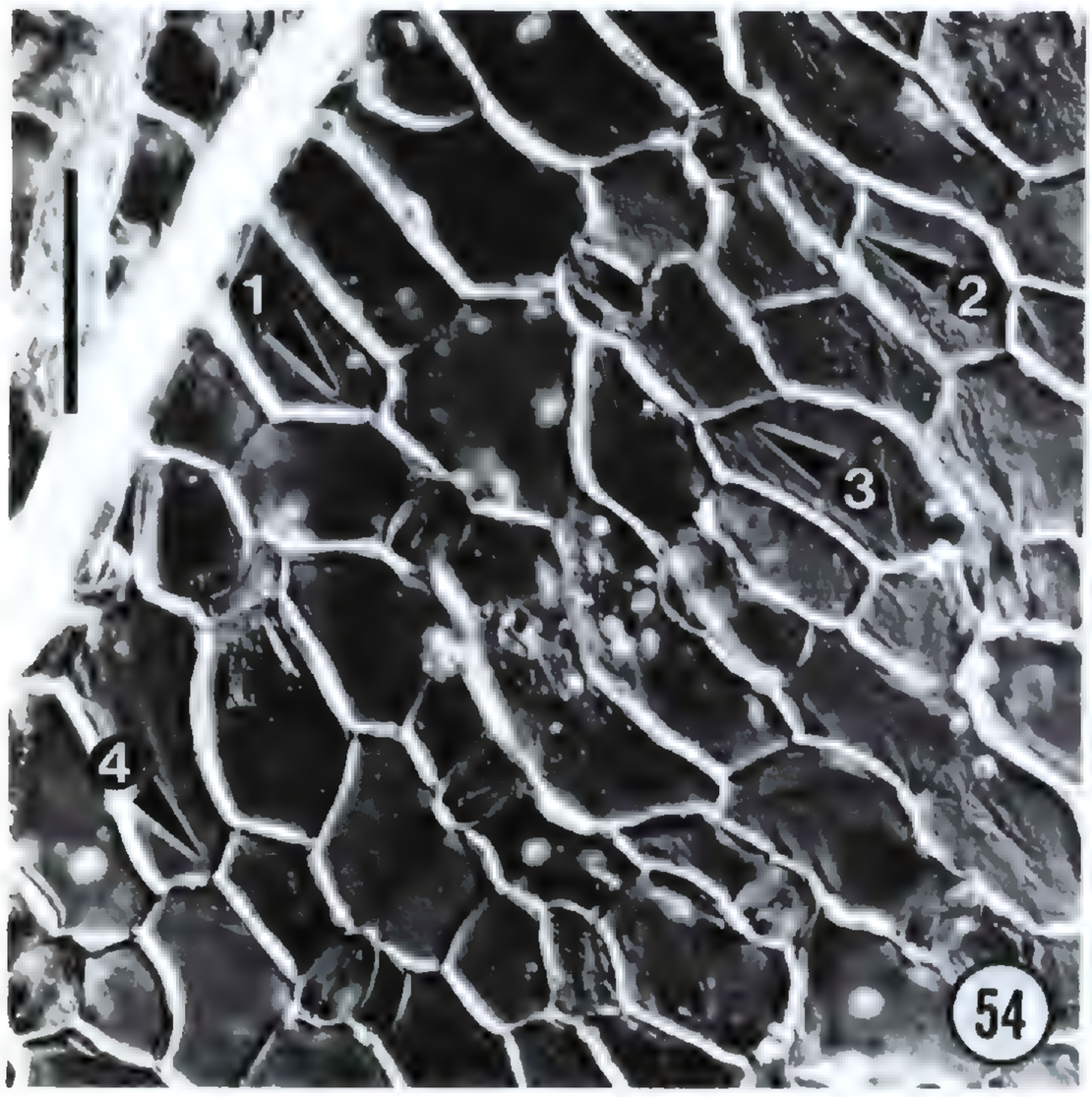
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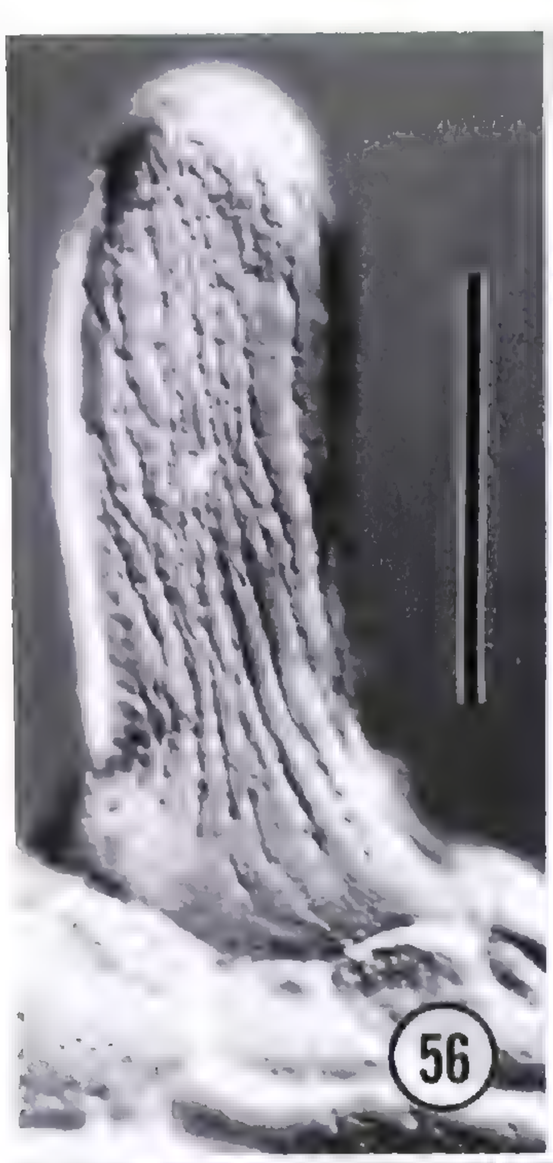
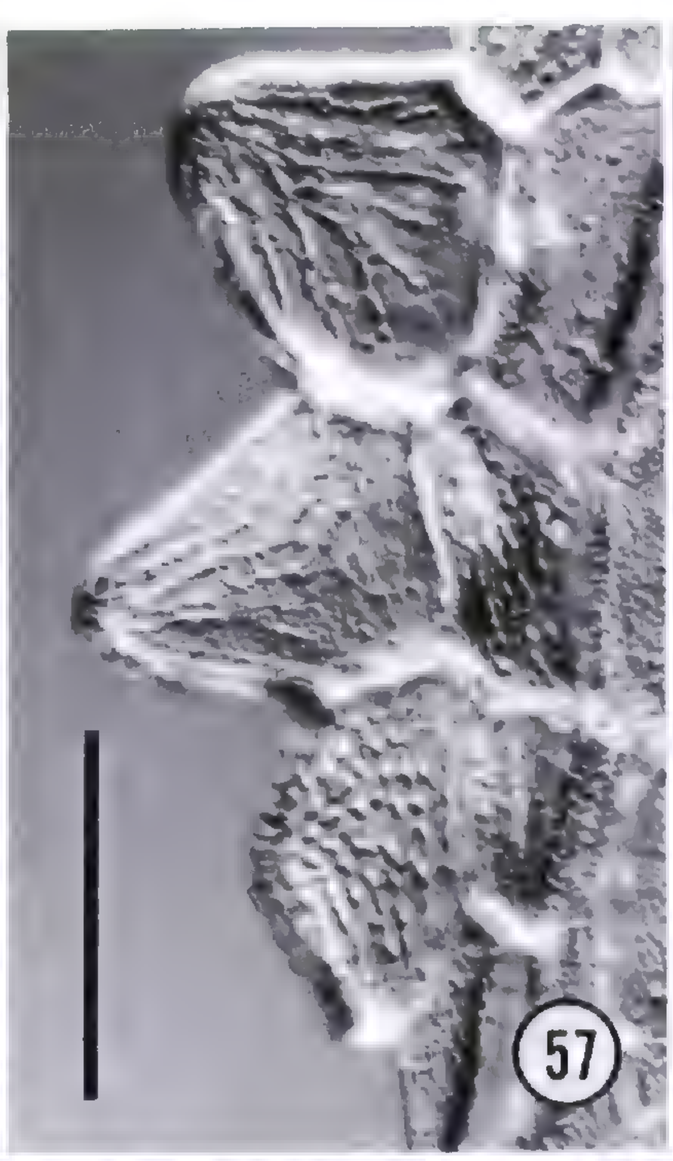
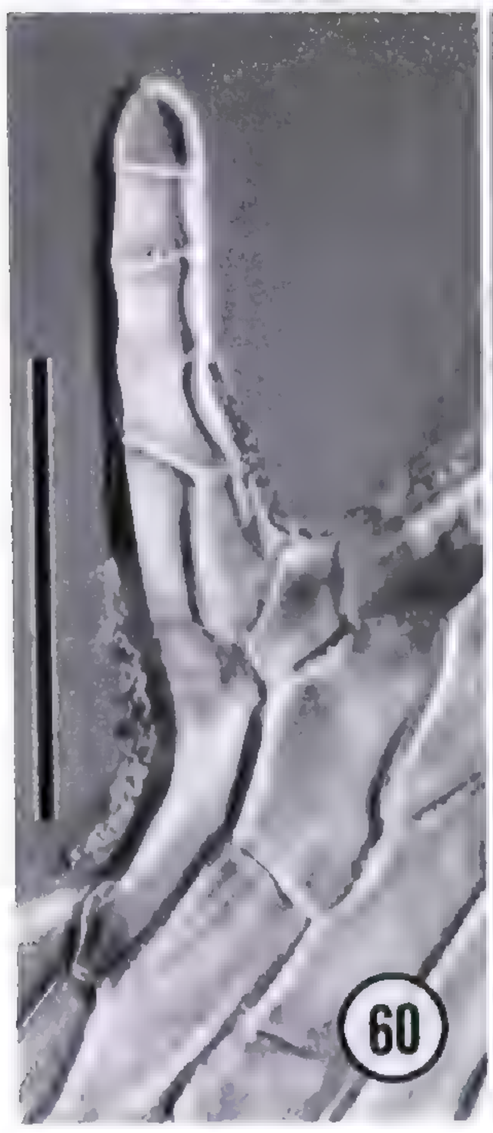
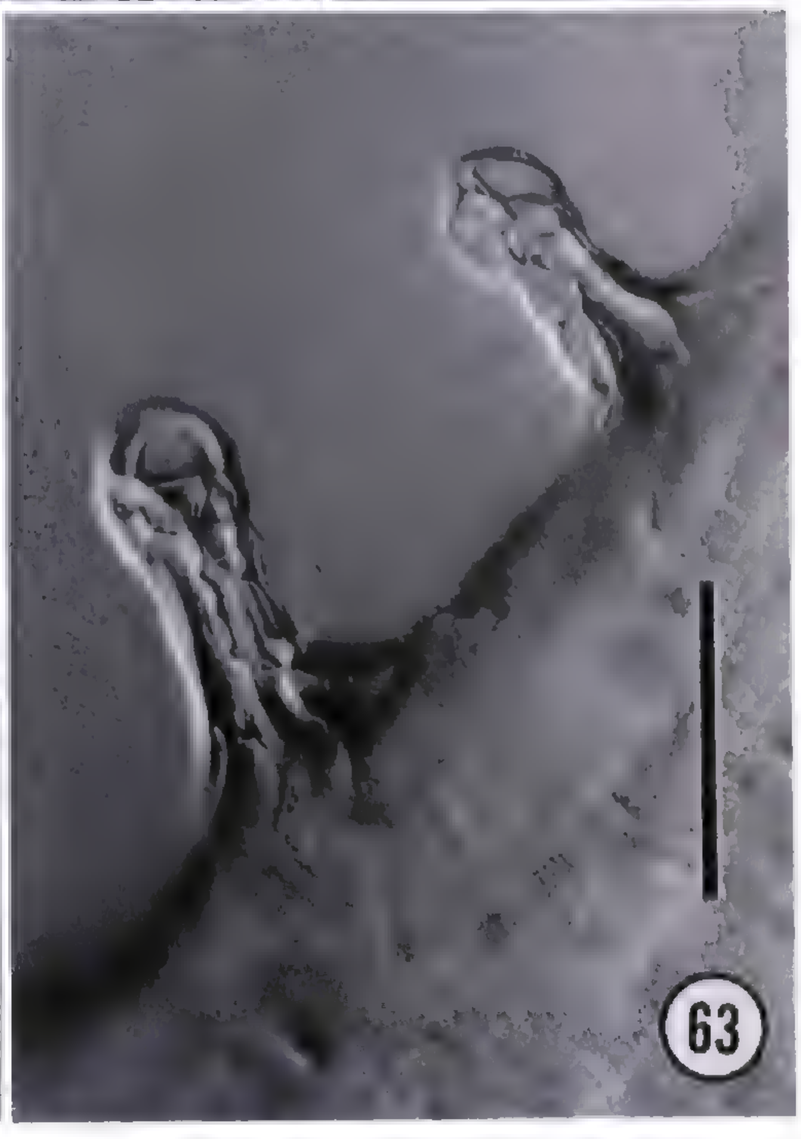




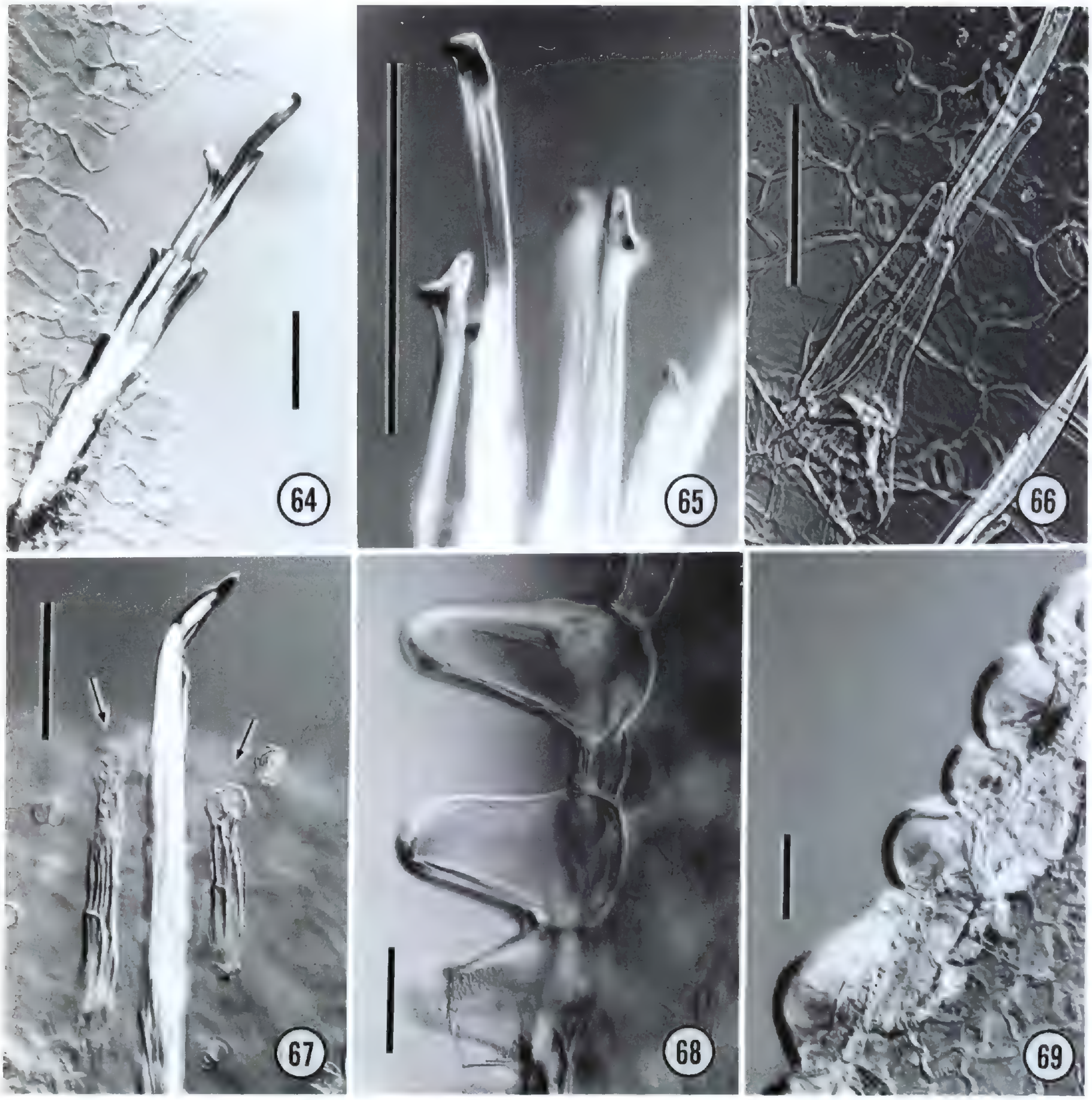



FIGURES 56–63.[1] Epidermal preparations of *Calandrinia* sects. *Calandrinia* and *Monocosmia* and *Montiopsis* subg. *Dianthoideae*. —56. Ribbed unicellular hair in *C.* (*Calandrinia*) *breweri* (*Hoover 6697*).—57. Ribbed unicellular papillae in *C.* (*Calandrinia*) *breweri* (*Hoover 6697*). —58. Ribbed unicellular hairs and papillae in *C.* (*Acaules*) *carolinii* (*Venturi 4824*).—59. Ribbed unicellular papillae in *C.* (*Monocosmia*) *monandra* (*Joseph 3719*). 60–62. Trichomes in *M.* (*Dianthoideae*) *andicola* (*Hastings 488*). —60. Multicellular trichome, multiseriate towards base and uniseriate towards tip.—61. Multiseriate-multicellular trichome.—62. Branched multiseriate-multicellular trichome.—63. Glandular multiseriate-multicellular trichomes in *M.* (*Dianthoideae*) *gayana* (*Sleumer 1219*). All scale bars = ca. 100 μm.

with Kelley's data, but she reported papillae in the species of *Calandrinia* sect. *Acaules*.

Figures 56–67 illustrate trichome types in *Calandrinia* and *Montiopsis*; for comparison, Figures 68 and 69 illustrate trichomes/papillae in *Rumicastrum* and *Montia*. Trichome presence and gross morphology was evaluated for all examined herbarium specimens and studied in detail in epidermal preparations (see Table 1).

All examined specimens of *C.* sect. *Calandrinia* possess unicellular ribbed trichomes (Fig. 56), as reported by Kelley (1973). The trichomes may be up to ca. 600 μm long but are sometimes merely papillar (Fig. 57). Unlike papillae in other genera (e.g., *Cistanthe*, Hershkovitz, 1991a; and *Montia*, Fig. 69), the outer tangential cell wall has a distinct U- or V-shaped process rather than a more generalized swelling. Thus, I distinguish between trichomes (process as long as or longer than broad), papillar trichomes (process broader than long), and




FIGURES 64–69.[4] Epidermal preparations of *Montiopsis* subg. *Montiopsis*, *Rumicastrum* sp., and *Montia parvifolia*.—64. Multiseriate barbed trichome in *Montiopsis* (*Montiopsis*) *capitata* (*Fischer 169*).—65. Macerated trichome of *Montiopsis* (*Montiopsis*) *umbellata* (*Joseph 3865*) showing barbed tips of individual hair cells.—66. Base of multiseriate barbed trichome of *Montiopsis* (*Montiopsis*) *parviflora* (*Johnston 5882*) showing elongate, undivided hair cells.—67. Glandular multiseriate-multicellular trichomes (arrows) in *Montiopsis* (*Montiopsis*) *copiapina* (*Johnston 6069*).—68. Unicellular unribbed papillae in *Montia parvifolia* (*Calder et al. 14865*).—69. Unicellular unribbed papillae in *Rumicastrum* sp. (Unvouchered specimen K-242, courtesy of Walter A. Kelley.) All scale bars = ca. 100 μm.

papillae (without a distinct process). I regard as papillar trichomes papillae sensu Peralta (1988; re: *Calandrinia*) and Gerbaulet (1992; re: *Anacampseros*, etc.). The trichomes and papillar trichomes of *Calandrinia* may sparsely or densely populate the leaf margin and may occur severally adjacent (Fig. 57).

Leaves in members of *C.* sect. *Acaules* are glabrous or bear unicellular ribbed trichomes and/or papillar trichomes identical to those found in *C.* sect. *Calandrinia*, e.g., *C. carolinii* (Fig. 58). Whether these trichomes are glandular, as interpreted by Carolin (1987; see also Peralta, 1988), could not be determined in the present investigation. Structurally, however, the unicellular trichomes of *C.* sect. *Acaules* are distinct from the multicellular and obviously glandular trichomes of *Montiopsis* (see below). Trichome presence varies within species *C. affinis*, *C. carolinii*, *C. caespitosa*, and *C. compacta*. They may occur through-

TABLE 3. Leaf traits of *Calandrinia* and *Montiopsis* and their distribution in other Portulacaceae. Rare states (i.e., states characteristic of one or two species in a taxon) are indicated in parentheses. The western American Portulacaceae (cf. Hershkovitz, 1991a, 1993) and *Rumicastrum* are listed by genus and the eastern American/African Portulacaceae are listed as a single entry. Basellaceae, Cactaceae, Didiereaceae, and *Amphipetalum* are, cladistically, members of the eastern American/African group but were not included in the cladistic analysis (see Hershkovitz, 1993). Nonetheless, the data for the eastern American/African taxa reflect, to the degree known, the traits of these excluded taxa. I have not adequately investigated Hectorellaceae and hence have not included data for this family. "Brachyparacytic" stomata are here intended to include all variants (e.g., amphibrachyparacytic) except brachytetracytic/staurocytic (see Hershkovitz, 1991a). The trichome data refer to foliar trichomes, including papillar trichomes, only and not axillary trichomes present in some eastern American/African Portulacaceae (see Hershkovitz, 1993), nor papillae. Sources for data not derived from the present text are listed in Hershkovitz (1993, appendix 1).

| Taxon | Petioles winged (if present) | Leaf base clasping | Leaf base jointed | Primary vein weak at apex | Fimbrial vein | Fimbrial vein perpendicular at apex | Typical stomatal type | Typical number of contact cells | Outer cycle of subsidiary-like cells | Unicellular trichomes | Trichomes ribbed | Multicellular trichomes | Glandular multicellular trichomes | Multiseriate trichomes |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calandrinia* § *Calandrinia* | + | + | + | + | + | + | brachytetra-/staurocytic | 4–5 | + | + | + | − | − | − |
| *Calandrinia* § *Acaules* | N/A | + | + | +/− | +/− | + | brachytetra-/staurocytic (brachyparacytic) | 4–5 | +/− | + (−) | + (N/A) | − | − | − |
| *Calandrinia* § *Monocosmia* | + | + | + | + | + | + | brachytetra-/staurocytic | 4–5 | + | + (−?) | + | − | − | − |
| *Montiopsis* subg. *Montiopsis* | N/A | + | + | − | − | N/A | brachyparacytic (anomocytic) | 4–5 | − | − | − | + | +/− | + |
| *Montiopsis* subg. *Dianthoideae* | N/A | + | + | − | − | N/A | brachyparacytic (brachytetra/staurocytic) | 4–5 | − (+) | − | − | + | + | + |
| *Claytonia* | + | + | + | − | + | − | brachyparacytic | 4–5 | − | − | N/A | − | − | − |
| *Montia* | + | + | + | − | + | − | brachyparacytic, anomocytic (brachytetra-/staurocytic) | 4–5 | − | − | N/A | − | − | − |
| *Cistanthe* | + | + | + | + | − | N/A | brachyparacytic (anomocytic) | 4–5 | − | − | N/A | − | − | − |
| *Lenzia* | N/A | + | + | − | − | N/A | brachyparacytic | 4–5 | − | − | N/A | − | − | − |
| *Lewisia* | N/A (+) | + | + | − | − | N/A | laterocytic (brachypara-, anomocytic) | 5–7 (4) | − | − | N/A | − | − | − |

TABLE 3. Continued.

| Taxon | Petioles winged (if present) | Leaf base clasping | Leaf base jointed | Primary vein weak at apex | Fimbrial vein | Fimbrial vein perpendicular at apex | Typical stomatal type | Multicellular tri-chomes | Glandular multicellular tri-chomes | Multiseriate tri-chomes | Typical number of contact cells | Outer cycle of subsidiary-like cells | Unicellular tri-chomes | Tri-chomes ribbed |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rumicastrum* | N/A (+) | – | – | +/– | – | N/A | anisocytic? (brachyparacytic) | – | – | – | 3 (4) | – | – (+?) | – |
| Eastern American/ African group | –, N/A | – | – | +/– | – | N/A | nonbrachypara-/ parallelocytic (brachytetracytic in *Schreiteria*) | – (+ in *Amphi-petalum*) | – | – | 3 (4) | – | +/– | – |

out the abaxial leaf surface of *C. graminifolia*. Trichomes are apparently absent in *C. acaulis* from Ecuador northwards, occur occasionally in Bolivian and Peruvian specimens, and are present in all three examined Argentinian herbarium specimens ("*C. saltensis*"). In effect, trichomes occur in *C. acaulis* only in its range overlap with *C. carolinii*. My observations of variable trichome presence in section *Acaules* are consistent with Peralta (1988) but not Kelley (1973), the latter reporting the absence of trichomes in all species.

The specimens of *C.* sect. *Monocosmia* (Fig. 59) possessed only unicellular ribbed papillar trichomes, which have a distinct U-shaped emergence.

The unicellular trichomes and papillar trichomes of *C.* sects. *Calandrinia*, *Acaules*, and *Monocosmia* are distinct from those of other Portulacaceae, e.g., *Rumicastrum* sp. (Fig. 68), in bearing ribs. As I have noted, I regard unicellular epidermal emergences in some Portulacaceae, e.g., *Montia parvifolia* (Fig. 69) and *Cistanthe* spp. (Hershkovitz, 1991a), as papillae rather than trichomes.

Foliar trichomes in *M.* subg. *Dianthoideae* are multicellular and range from uniseriate (Fig. 60; only the basal cell is biseriate) to multiseriate (Fig. 61) to branched multiseriate (Fig. 62). If present, branched multiseriate trichomes typically occur along the leaf base margins and intergrade with vascularized leaf dentations (see above). The uniseriate trichomes tend to occur along the leaf margin, although in some specimens they occur occasionally on the lamina. Glandular trichomes are present or absent in *M. andicola* and *M. gayana* (Fig. 63). Some specimens of *M.* subg. *Dianthoideae* appear to be glabrous. While my observations on trichome structure in subgenus *Dianthoideae* agree with earlier reports (Kelley, 1973; Peralta, 1988), the material I examined includes what I presume to be a disproportionate number of glabrous or nearly glabrous specimens of otherwise pubescent species.

Leaves (and sepals) of all examined species of *M.* subg. *Montiopsis* bear distinctive multiseriate trichomes composed of long intertwined hair cells. Ford (1992) noted that, in some species, the tips of the individual hair cells are bent outward so that the trichome appears barbed (Fig. 64). The individual hair cells may also be barbed at the tip (Fig. 65). According to Kelley (1973), the multiseriate trichomes are several cells long, i.e., the individual hair cells are transversely divided. In the present study, individual hair cells traced to their point of origin at the leaf surface (Fig. 66) did not show evidence of transverse walls. Apparently the hair

TABLE 4. Foliar characters, character states, and scores for Portulacaceae used in the present cladistic exercise. The character numbers accord with, and the character analyses are provided in, Hershkovitz (1993: appendix 1). Polarities, where presumed, are scored as "0" in the hypothetical ancestor. The "0" designation also denotes a posteriori determined primitive states. Otherwise, the state designations are arbitrary. "X" character states are employed following Doyle & Donoghue (1986) and are analyzed as missing data in PAUP. Other missing data scores are denoted as "?" (unknown) or "V" (too variable within the OTU to determine). Character states variable within an OTU but scored for the presumed primitive state are underlined in the data matrix.

7. Leaves alternate, 0; leaves opposite, 1.
8. Leaf bases jointed, 0; leaf bases not jointed, 1.
9. Leaf bases clasping, 0; leaf bases not clasping, 1.
10. Leaf mucilage cells conspicuous and relatively numerous, 0; leaf mucilage cells none or few and not conspicuous and few, 1.
11. Ribbonlike veins absent, 0; ribbonlike veins present, 1.
12. Leaf venation not festooned brochidodromous, 0; leaf venation festooned brochidodromous, 1.
13. Fimbrial vein absent, 0; fimbrial vein present, 1.
14. Fimbrial vein becoming perpendicular to the primary vein at the apex, 0; fimbrial vein parallel to the primary vein at the apex, 1; fimbrial vein absent, X.
15. Stomata predominantly brachyparacytic and/or and similar types (see Hershkovitz, 1991a), 0; stomata predominantly parallelocytic and/or nonbrachyparacytic, 1.
16. Stomata predominantly brachyparacytic, nonbrachyparacytic, or parallelocytic, 0; stomata commonly brachytetracytic and/or staurocytic, 1.
17. Foliar trichomes absent, 0; foliar trichomes present, 1.
18. Trichomes unicellular, 0; trichomes multicellular, 1.
19. Trichomes uniseriate, 0; trichomes multiseriate, 1.
20. Trichomes nonglandular, 0; trichomes glandular, 1.
21. Trichomes nonribbed, 0; trichomes ribbed, 1; trichomes absent, X.

| OTU | 7 | 21 |
|---|---|---|
| Ancestor | 0???0?0X?0????X | |
| *Anacampseros* § *Anacampseros* | 0001000X1010000 | |
| *Anacampseros* § *Avonia* | 0001?00X1000000X | |
| *Anacampseros* § *Tuberosae* | 0001?00X101000X | |
| *Calandrinia acaulis* | 0110001001000OX | |
| *Calandrinia affinis* | 0110001001 10001 | |
| *Calandrinia caespitosa* | 0110000X0110001 | |
| *Calandrinia carolinii* | 0110001001 10001 | |
| *Calandrinia compacta* | 0110000X00 10001 | |
| *Calandrinia* § *Monocosmia* | 0110001001 10001 | |
| *Calandrinia* § *Calandrinia* | 0110001001 10001 | |
| *Calyptrotheca* | 000???0X100000X | |
| *Ceraria* | 1001010X100000X | |
| *Cistanthe* § *Amarantoideae* | 011?1 10X000000X | |
| *Cistanthe* § *Calyptridium* | 011?1 10X000000X | |
| *Cistanthe* § *Cistanthe* | 011V1 10X000000X | |
| *Cistanthe* § *Philippiamra* | 011?1 10X000000X | |
| *Cistanthe* § *Strophiolum* | 011?010X000000X | |
| *Claytonia* | 0110001 1000000X | |
| *Grahamia* | 000?100X100000X | |
| *Lenzia* | 011?000X000000X | |
| *Lewisia* | 0110000X000000X | |
| *Montia* (excl. § *Naiocrene*) | 0110001 1000000X | |
| *Montia* § *Naiocrene* | 0110001 1010000X | |
| *Montiopsis* § *Dianthoideae* | 0110000X0011110 | |
| *Montiopsis* § *Montiopsis* | 0110000X0011110 | |
| *Portulaca* | V001010X100000X | |
| *Portulacaria* | 1001000X100000X | |
| *Rumicastrum* | 000?100X?000000X | |
| *Schreiteria* | 000?100X010000X | |
| *Talinaria* | 0001000X100000X | |
| *Talinopsis* | 100?100X100000X | |
| *Talinum* § *Phemeranthus* | 0001100X100000X | |
| *Talinum* § *Talinum* | 0001110X1010000 | |

TABLE 4. Continued.

cells divide infrequently, if at all (cf. Becker, 1895). In any case, these trichomes sparsely populate or, in some species, densely cover the leaf surface and may be as long as ca. 3 mm. I found glandular trichomes resembling those of *M.* subg. *Dianthoideae* in only one specimen of *M.* subg. *Montiopsis* (*M. copiapina*, Fig. 67), but they have been reported in several other species (Ford, 1992; Kelley, 1973). The glandular trichomes ranged from few-celled and uniseriate to multiseriate. Unlike the eglandular trichomes, the elongate cells of the multiseriate-glandular trichomes are clearly transversely divided.

### B. PHYLOGENETIC ANALYSIS

Table 3 compares the foliar traits of *Calandrinia* and *Montiopsis* with those found in other Portulacaceae. Only those traits of *Calandrinia* and *Montiopsis* that are differentially distributed among other Portulacaceae are listed, e.g., linear leaves occur in most genera of the family and hence are not listed. Figure 70A and B compares consensus trees derived from cladistic analysis of all (from Hershkovitz, 1993) versus only nonfoliar characters, respectively. Figure 71 is a consensus derived from trees generated using weighted foliar characters. The OTU definitions, data, and character analyses are presented elsewhere (Hershkovitz,

TABLE 5. Tree statistics for Figures 70A, B and 71. Listed below are the lengths, consistency indices (CI), and rescaled consistency indices (RC) for all characters, foliar characters, and nonfoliar characters for the trees used to generate the consensuses in Figures 70A, B and 71. The statistics vary among the different trees used to generate Figure 70A when considering only the character subsets. Note that CI and RC vary inversely with respect to tree length for the character subsets for Figure 70A.

| Consensus tree | Length (all characters) | CI | RC | Length (foliar characters) | CI | RC | Length (nonfoliar characters) | CI | RC |
|---|---|---|---|---|---|---|---|---|---|
| Figure 70A | 107 | 0.449 | 0.346 | 29–32 | 0.517–0.469 | 0.441–0.385 | 75–78 | 0.440–0.423 | 0.326–0.306 |
| Figure 70B | 108 | 0.444 | 0.341 | 34 | 0.441 | 0.353 | 74 | 0.446 | 0.333 |
| Figure 71 | 121 | 0.397 | 0.284 | 25 | 0.600 | 0.537 | 96 | 0.344 | 0.210 |

1993), but, for convenience, the foliar data scores are listed in Table 4. Figures 70 and 71 do not show the speculative positions of Basellaceae, Cactaceae, Didiereaceae, or *Talinella* (cf. Hershkovitz, 1993, fig. 1). Table 5 lists the lengths, consistency indices (CI) and rescaled consistency indices (RC) of the trees on which the consensuses are based. For each treefile, the tree statistics for all, just foliar, and just nonfoliar characters are compared. Not all of the characters listed in Table 3 were included in the cladistic analysis (see Hershkovitz, 1993, appendix 1): petiolar morphology, primary vein morphology at the leaf apex, and the presence of an outer cycle of subsidiary-like cells were excluded.

Figures 70B and 71 were each independently derived by two procedures: (1) searching under various PAUP modes (Swofford, 1991; see Hershkovitz, 1993) using weights of 100 for the nonfoliar and foliar character sets, respectively, followed by weight equalization to derive comparable tree statistics; and (2) searching using only the desired character set, followed by restoration of the excluded characters and screening for the shortest trees. The aim in the latter procedure was to recover the shortest trees based on the included data that were otherwise most consistent with the excluded data. The dashed lines in Figures 70B and 71 denote nodes not supported by at least one nonfoliar or foliar character state change, respectively. These branches would be collapsed in a consensus of all trees generated using nonfoliar or foliar characters exclusively.

I aborted the searches using weighted nonfoliar characters when 9,000 trees were saved. Inasmuch as the consensus of these trees (Fig. 70B) is similar to that of trees generated using all characters equally weighted (Fig. 70A), I suspect that the number of equally parsimonious trees is actually more than an order of magnitude greater (cf. Hershkovitz, 1993). Despite their similarity, the consensuses compared in Figure 70 are based on completely different sets of trees: those yielding Figure 70A are 107 steps, and those yielding Figure 70B are, over all characters, 108 steps. Nevertheless, the unambiguous character state changes defining the nodes in Figure 70B are essentially those defining the nodes in Figure 70A (see Hershkovitz, 1993) minus those that become ambiguous when some nodes are collapsed. Hence, I do not show the unambiguous character state changes on the Figure 70B tree.

The consensus in Figure 71 is based on 490 trees found using weighted foliar characters and PAUP's tree bisection/reconnection algorithm to completion. The unambiguous foliar character state changes are indicated and numbered according to Hershkovitz (1993, appendix 1).

## DISCUSSION

### 1. TAXONOMIC SIGNIFICANCE OF FOLIAR MORPHOLOGY IN *CALANDRINIA* AND *MONTIOPSIS*

*A. Phenetic comparison of foliar traits of* Calandrinia *and* Montiopsis. Table 3 emphasizes the degree of homogeneity of foliar morphology within *Calandrinia* and *Montiopsis*, the distinctions in foliar morphology between these genera and other western American Portulacaceae, and the additional distinctions between these genera and eastern American/African Portulacaceae (cf. Hershkovitz, 1993).

*Calandrinia* is distinguished by the combination of the fimbrial vein that overtops and becomes perpendicular to the primary vein at the leaf apex, the predominance of brachytetracytic/staurocytic stomata commonly with an outer cycle of subsidiary-like cells, and unicellular-ribbed trichomes. These features are absent in some species of *Cal-*

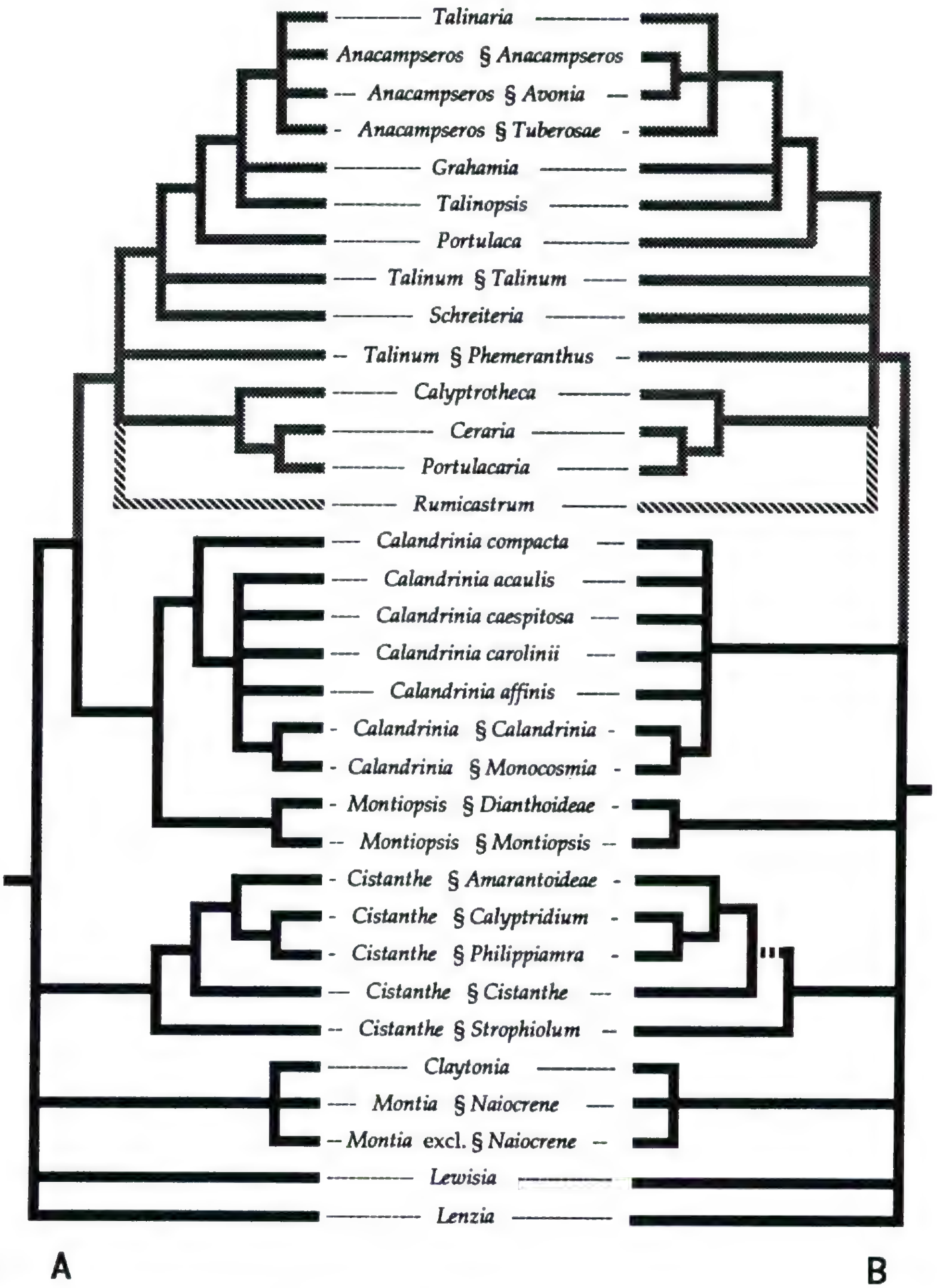



FIGURE 70. Juxtaposed consensuses of cladograms of Portulacaceae generated using all characters equally weighted versus weighted nonfoliar characters. Table 5 lists length and consistency statistics. Shaded branches delineate the eastern American/African taxa (Hershkovitz, 1993), and the diagonally hatched branch denotes Australian endemism.—70A. Consensus of cladograms of Portulacaceae generated using equally weighted foliar and nonfoliar characters. This consensus and its unambiguous character state changes are discussed and illustrated elsewhere (Hershkovitz, 1993: fig. 1). The speculated positions of Basellaceae, Cactaceae, Didiereaceae, and *Talinella*, however, are here omitted.—70B. A consensus of trees generated by 100-fold weighting of 31 nonfoliar characters from Hershkovitz (1993: table 3 and appendix 1, chars. 1–6 and 22–46). The consensus is compatible with trees generated using nonfoliar characters exclusively. All except the dashed branch are at least equivocally supported by at least one nonfoliar character state change. The dashed branch is supported only by a foliar character state change. The unambiguous character state changes in Figure 70B include those indicated elsewhere for Figure 70A (Hershkovitz, 1993: fig. 1) minus those that become ambiguous because of decreased resolution.

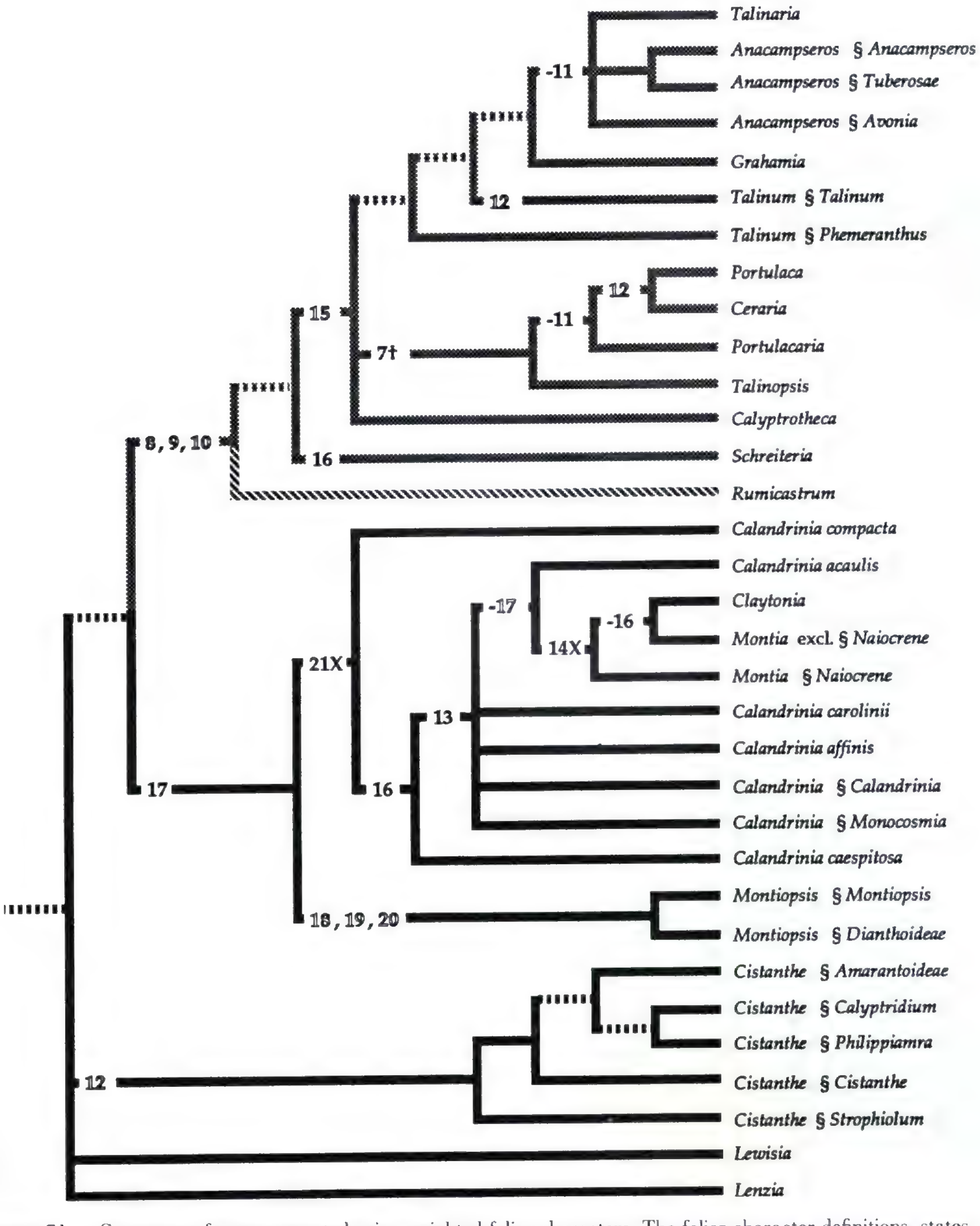



FIGURE 71. Consensus of trees generated using weighted foliar characters. The foliar character definitions, states, and OTU scores are reproduced in Table 4. Table 5 lists length and consistency statistics. Shaded branches delineate the eastern American/African taxa (Hershkovitz, 1993), and the diagonally hatched branch denotes Australian endemism. The trees were generated by 100-fold weighting of 15 foliar characters from Hershkovitz (1993: table 3 and appendix 1, chars. 7–21) and, independently, by using foliar characters exclusively, followed by reinstatement of nonfoliar characters and filtering for the shortest trees. Unambiguous foliar character state changes are indicated. Polarized characters are shown in black and unpolarized in white. "X" and "†" indicate that OTUs at adjacent branches were scored as missing data ("?") because of "X" character definitions or uncertainty (see Table 4). All except the dashed branches are at least equivocally supported by at least one foliar character state change. The dashed branches are supported only by nonfoliar character state changes.

*andrinia* sect. *Acaules*, however. Fimbrial veins, although morphologically distinct, characterize *Claytonia* and *Montia*, and brachytetracytic stomata characterize one species of the latter. Brachytetracytic stomata also regularly occur in *Montiopsis* subg. *Dianthoideae*, *Schreiteria*, and occasionally among other stomatal types in *Cistanthe* (Hershkovitz, 1991a). Trichomes occur in other Portulacaceae but are not ribbed and, in *Montiopsis* and *Amphipetalum* Bacigalupo (in Spichiger, 1988), are multicellular. Glandular or eglandular multiseriate trichomes are restricted to *Montiopsis* and represent the sole foliar distinction between this genus and other Portulacaceae.

Both *Calandrinia* and *Montiopsis* share with other western American Portulacaceae their leaf base and petiolar morphology and stomatal contact cell number. These features are generally not present in eastern American/African Portulacaceae. Well-differentiated petioles are absent in *C.* sect. *Acaules*, however. One species of *Rumicastrum* ("*Calandrinia pumila* F. Muell.") has both winged petioles and brachyparacytic stomata with four contact cells (Hershkovitz, unpublished).

The relatively pronounced diminution and/or distal ramification of the leaf primary vein in *Calandrinia* sects. *Calandrinia*, *Monocosmia*, and species of section *Acaules* may provide a synapomorphy for all or part of the genus. In some members of Portulacaceae, e.g., *Lewisia*, the primary vein is always prominent and/or unramified at the leaf apex, whereas other taxa, e.g., *Cistanthe* and various eastern American/African Portulacaceae, always have apically weak to indistinct primary veins (Hershkovitz, 1991a, unpublished). Some taxa, however, are intermediate for this feature, and evaluation of primary vein diminution is somewhat subjective.

Traits not compared in Table 3 include dentate leaf margins, the number of distinct vein orders, and the number of veinlets in the ultimate enclosures. The dentate leaf margins that characterize *Montiopsis* subg. *Dianthoideae* are here regarded as unique. Dentate leaf margins in species of *Lewisia* occur toward the apex of the leaf, rather than, as in *M.* subg. *Dianthoideae*, at the extreme base. I have not scrutinized veinlet numbers throughout Portulacaceae. Nevertheless, the paucity of freely ending veinlets might reinforce the relationship between *Calandrinia* sects. *Calandrinia* and *Monocosmia*, because veinlet numbers are higher among members of *C.* sect. *Acaules*. The poor differentiation and/or low number of distinct vein orders of *Calandrinia* characterize similar-sized leaves in species of several genera throughout Portulacaceae.

*B. Phylogenetic analysis of foliar traits of* Calandrinia *and* Montiopsis. The purpose of the cladistic exercise in this study was to evaluate the degree of taxonomic utility of foliar characters, in particular for clarifying the systematics of *Calandrinia* and *Montiopsis*. The degree of agreement between phylogenetic estimates based on foliar versus nonfoliar characters might be taken as a reliability index of each character set, and the ability of the foliar set to provide additional resolution or "break ties" in analyses based on the nonfoliar set might be taken as a measure of complementarity. If the character sets suggest conflicting phylogenetic resolutions, the data set providing the greatest degree of congruence with all characters combined might be regarded as superior. Evaluation of the utility of foliar versus nonfoliar characters requires additional considerations as well, however, including the size of the respective data sets and the degree to which each taxon has been investigated.

Superficially, the cladistic analysis suggests that the foliar data tend to misinform. The Figure 71 consensus tree derived from analysis of weighted foliar characters shows significant similarities but also departures from the consensuses of trees generated using all characters (Fig. 70A) or weighted nonfoliar characters (Fig. 70B). When measured with all characters equally weighted, the trees generated with weighted foliar characters are 13% longer than those generated with equal weightings (Table 5). In contrast, the consensuses of the Figure 70A and 70B are nearly identical even though the sets of trees used to generate each consensus are necessarily mutually exclusive. Thus, the analysis suggests that the foliar characters are somewhat dispensable. These results must be evaluated in the context of results for individual subclades and characters.

The foliar versus nonfoliar data suggest rather different relationships for *Calandrinia* and *Montiopsis*. The nonfoliar data (Fig. 70B) indicate that *Calandrinia* is monophyletic and possibly (but not necessarily) the sister group of *Montiopsis*, and that *Calandrinia* sects. *Calandrinia* and *Monocosmia* are sister groups. The foliar data (Fig. 71) indicate that *Calandrinia*—with *Claytonia* and *Montia* nested therein—is a sister group to *Montiopsis*, and that sections *Calandrinia* and *Monocosmia* may not be sister groups. In both consensuses, *Montiopsis* is monophyletic. The combined

data (Fig. 70A) agree more with the nonfoliar data, conserving only the *Calandrinia* + *Montiopsis* clade suggested by the foliar data.

Scrutiny of Figure 71 reveals that both the *Calandrinia* + *Montiopsis* clade and the inclusion of *Claytonia* and *Montia* therein are not strongly supported even by the foliar data. The sole synapomorphy of the *Calandrinia* + *Montiopsis* clade is the derivation of trichomes (char. 17), which, as I have noted, are structurally distinct in the two groups. My character definition and scoring in this case was intended to permit trichomes to be homologous in the two groups unless contradicted by other evidence. In the case of Figure 70A (see Hershkovitz, 1993) and Figure 71, it is neither contradicted nor independently supported. Likewise, the inclusion of *Claytonia* and *Montia* reflects my effort, via the use of "X" characters (Doyle & Donoghue, 1986; Hershkovitz, 1993), to permit the structurally distinct fimbrial veins (char. 13) in the two groups to be homologous and also, via recognizing *Montia* sect. *Naiocrene* as a distinct OTU, to allow the homology of brachytetracytic/tetracytic stomata (char. 16). These characters provide the sole evidence for the inclusion of *Claytonia* and *Montia* within *Calandrinia*, and brachytetracytic/staurocytic stomata must then be lost in *Claytonia* and most *Montia* species.

While the foliar evidence provides at least some support for the inclusion of *Claytonia* and *Montia* within *Calandrinia*, excluded foliar evidence might refute it. I did not include petiole presence in my analyses because all OTUs with petiolate taxa include taxa without petioles. Petioles characterize *Calandrinia* sect. *Monocosmia*, all species of section *Calandrinia* (although variable within species of the latter), *Montia* sect. *Naiocrene*, and several species of *Claytonia* and the remaining *Montia* sections. Petioles are lacking (or hardly distinct) in *Calandrinia* sect. *Acaules*. In the context of Figure 71, this evidence could provide a synapomorphy for *Calandrinia* sects. *Calandrinia* and *Monocosmia* and would appear to cause *Claytonia* and *Montia* to become, at least equivocally, a sister group of the first two or fall out of the *Calandrinia* clade altogether. The only robust clades that would remain would be those supporting a close relationship between the sections of *Calandrinia* and the monophyly of *Claytonia* + *Montia* (cf. Fig. 70B).

For other Portulacaceae, cladistic analysis of foliar versus nonfoliar characters also yields only partial congruence. Figures 70B and 71 concur in diagnosing the monophyly of *Claytonia* + *Montia*, *Montiopsis*, the eastern American/African group + *Rumicastrum*, and *Anacampseros* + *Talinaria* (see also Gerbaulet, 1992). For *Montiopsis* and the eastern American/African group + *Rumicastrum*, the foliar evidence provides substantial corroboration of nonfoliar evidence (Fig. 71; cf. Hershkovitz, 1993, fig. 1). The consensuses disagree regarding the precise relationships within the eastern American/African clade. Reconciliation of these disagreements is beyond the scope of the present paper: I have not adequately scrutinized either the taxonomy or leaf morphology of the eastern American/African group for this purpose. The apparent concurrence between Figures 70B and 71 regarding the monophyly of *Cistanthe* is artificial. Analysis with weighted foliar characters yields the result shown in the Figure 71 consensus in which brochidodromous leaf venation is a synapomorphy of *Cistanthe*. This evidence becomes equivocal using foliar characters only (i.e., by collapsing the dashed branches in Fig. 71). Thus, the foliar evidence complements the nonfoliar for diagnosing monophyly of *Cistanthe* (cf. Hershkovitz, 1993, fig. 1).

A peculiar result of the present analysis is that the *Calandrinia* + *Montiopsis* + eastern American/African group + *Rumicastrum* clade is supported in all trees generated using all (Fig. 70A) or weighted foliar characters (Fig. 71). This clade is equivocal in the nonfoliar consensus (Fig. 70B); hence one might surmise that the clade must be supported by a foliar character. In fact, the only character supporting this topology in Fig. 70A is the derivation of panaperturate pollen (see Hershkovitz, 1993). The reason that the clade appears unequivocal in the foliar weighted trees is because no evidence contradicts the homologization of trichomes in *Calandrinia* + *Montiopsis*. As a result, panaperturate pollen becomes equivocally primitive in *Montiopsis*, which then forces the homology with equivocally primitive panaperturate pollen in the eastern American/African group + *Rumicastrum*. I fortuitously discovered that scoring *Calandrinia caespitosa* as absent for trichomes is sufficient to cause, among other things, the *Calandrinia* + *Montiopsis* + eastern American/African group + *Rumicastrum* clade to become equivocal. That a minimal data modification can have such major ramifications should elicit caution in interpreting cladistic results, especially in this case because trichomes are only variably present in species of *Calandrinia* sect. *Acaules*.

It is possible that differences between the consensuses in Figures 70 and 71 reflect artifacts that might be expected given the structure of the data.

The foliar and nonfoliar data comprise, respectively, 15 and 31 characters for 33 taxa. A larger character set should yield a more reliable result, although the result should not necessarily differ from that using a smaller set. Perhaps consistent with this principle, the 31-character nonfoliar data consensus is more similar to the 46-character combined data set consensus than is the 15-character foliar data consensus. Yet, obviously contradicting the principle, the 31- and 46-character data sets yield virtually identical consensuses, despite the substantial difference in data set size.

Another consideration is the claim that, for a given number of taxa, the perceived consistency index (CI; = the number of apomorphic states in the data divided by the length of the cladogram; i.e., the degree of perceived homoplasy), should vary inversely relative to the number of characters in the data (Archie, 1989, 1990). Because the CI is often interpreted as a measure of the reliability of the data and accuracy of the tree, factors that artificially inflate the CI (in this case, a small character data base) should also distort the cladistic results. Alternatively, Sanderson & Donoghue (1989) found no decisive evidence of a relationship between the number of characters and the CI, although they agreed that the CI may not be a good indicator of cladogram accuracy. The data in Table 5 superficially appear to support the view of Archie (1989, 1990): the CI of trees generated using the smaller foliar data set is much higher than that of trees using the larger nonfoliar data set. The CI of trees generated using all 46 characters, however, is slightly greater than that of trees generated using 31 nonfoliar characters. Moreover, the CIs for individual foliar characters (i.e., the number of apomorphic states of the character divided by the number of state changes in the tree) are, in general, higher than for nonfoliar, even in trees generated using the combined data set (Table 5).

A possible artifact in the CI data arises when some characters vary in only a few OTUs, e.g., the trichome traits that are restricted to the two OTUs of *Montiopsis*. The CI for these three characters cannot possibly be lower than 0.5. In other words, irrespective of phylogeny, the maximum number of state changes for these characters is two. The CI of a binary character with ca. half of the OTUs like-scored can approach (but not equal) zero, e.g., if each apomorphic state is independently derived. Farris (1989) proposed a rescaled consistency index (RC), which adjusts for biases in character state frequencies, although Archie (1990) criticized this statistic. Because PAUP calculates RC and not Archie's (1989, 1990) proposed "homoplasy excess ratio," I list RC in Table 5. For the present data, the RCs are lower than but more or less parallel to the CIs, and the RCs of the nonfoliar rather than the foliar characters appear to be more depressed relative to the CIs. Perhaps this is not surprising: while some of the foliar character states vary among relatively few taxa, others, e.g., leaf base morphology (chars. 8, 9), have potentially very low but actually very high CIs.

More rigorous and sophisticated analyses are feasible for assessing the cladistic behavior of foliar versus nonfoliar characters in Portulacaceae, but the significance of foliar data should be clear from the evidence presented here. For example, the foliar evidence generally supports a close relationship among the sections of *Calandrinia* (the spurious results for *Claytonia* and *Montia* notwithstanding), the monophyly of *Montiopsis*, and, weakly, a sister group relationship between the last two genera (Fig. 71). These results are at least consistent with those based on nonfoliar data (Fig. 70B) and corroborate my earlier propositions (Hershkovitz, 1990, 1991b, 1993) regarding the systematics of *Calandrinia* and *Montiopsis*. Specifically, the foliar data support the close relationship of *Calandrinia* sect. *Monocosmia* to *Calandrinia* as proposed by Carolin (1987) and refute earlier taxonomic opinions on a close relationship between section *Monocosmia* and Cistanthe sect. *Calyptridium* (McNeill, 1974; Nyanyano, 1986a, 1990; Pax & Hoffmann, 1934). In supporting the coherence of *Calandrinia*, the leaf data also refute Carolin's (1987) results linking *Calandrinia* sects. *Calandrinia* and *Monocosmia* with *Rumicastrum*. The leaf data might be interpreted as supporting (or at least not refuting) Carolin's alternative proposal that *Calandrinia* sects. *Calandrinia* and *Monocosmia* are closely related to *Montia*. A close relationship between *Calandrinia* and *Claytonia* + *Montia* remains a possibility based on all characters (cf. Hershkovitz, 1993, table 4) although the precise relationship proposed by Carolin is probably incorrect. Although not the focus of the present paper, the leaf data also provide strong support for the distinction between the eastern American/African and western American Portulacaceae. Finally, analysis of the foliar versus nonfoliar data for Portulacaceae yields results consistent with opinions put forth elsewhere (e.g., Levin, 1986) that foliar characters are more conserved evolutionarily than implicit in traditional taxonomies emphasizing reproductive characters. Although the taxonomic utility of foliar characters is now widely appreciated (e.g., Cronquist, 1988: 176–184;

Takhtajan, 1991, chapter 1), the opinion that foliar and other vegetative organs "are characterized by more reversibility than reproductive organs" (Takhtajan, 1991: 21) persists. In fact, in the present study, the foliar characters proved to be more conserved than the nonfoliar in cladograms derived using all characters and about equally conserved as nonfoliar in cladograms in which the nonfoliar characters are exceedingly weighted. Of course, some foliar characters, e.g., petiole presence, were excluded from the analysis because they appear to be inherently homoplasious, but the same is true of some reproductive characters, e.g., stamen and ovule number.

## 2. DEVELOPMENTAL, FUNCTIONAL, AND EVOLUTIONARY CONSIDERATIONS OF FOLIAR MORPHOLOGY IN *CALANDRINIA* AND *MONTIOPSIS*

In my consideration of foliar morphology of *Cistanthe* (Hershkovitz, 1991a), I briefly discussed ideas put forth on the adaptive value of leaf shape, leaf venation pattern, and stomatal complex morphology. Those comments are applicable here. For *Calandrinia* and *Montiopsis*, the functional significance of trichomes must also be considered. In addition, models attempting to explain venation and epidermal patterning as a consequence of cellular-level physiological phenomena during early tissue differentiation must be reconciled in the light of detailed systematic studies of foliar morphology such as that presented here and elsewhere.

Givnish (1979) supposed that leaves not requiring much physical support should tend to have more parallel rather than pinnate venation in order to optimize vascular supply efficiency. As I noted previously (Hershkovitz, 1991a), venation in *Cistanthe* does not seem to conform to this expectation, nor does that of *Calandrinia* and *Montiopsis*. The largest/broadest leaves among these two genera are the basal leaves of *Calandrinia* sects. *Calandrinia* and *Monocosmia*—these lie more or less prostrate on the ground, hence require little internal support. Leaves of *Montiopsis* and *Calandrinia* sect. *Acaules* also seem to lack the need for much internal support because they tend to be succulent (at least relative to their dimensions) and may also lie prostrate on the ground. Yet, venation is basically pinnate in both genera, even in taxa with a more or less grasslike habit. The combination of the primary vein and well-developed fimbrial vein in *Calandrinia* sects. *Calandrinia* and *Monocosmia* and some species of section *Acaules* might be perceived as a sort of parallel venation pattern, but, in contrast to grasses and other taxa with parallel veins, the fimbrial vein is best developed toward the apex and is poorly to not at all distinct basally. The functional significance of the fimbrial vein itself is not clear. This structure could conceivably be associated with some type of leaf apical secretory function, but no obvious glandular structure was identified at the apex of these leaves. Whatever the functional significance of the fimbrial vein, some species of *Calandrinia* sect. *Acaules* appear to survive well without it.

As I noted previously (Hershkovitz, 1991a), the functional significance of stomatal complex morphology—specifically, the number, shape and arrangement of subsidiary cells—remains unknown; hence I can offer no explanation for the predominance of brachytetracytic/staurocytic stomata and partial to complete outer cycle of subsidiary-like cells in *Calandrinia* sects. *Calandrinia* and *Monocosmia* and species of section *Acaules*. Possibly the more or less radial rather than bilateral symmetry of the stomatal complex in these taxa underlies its functional significance. Again, the lack of brachytetracytic/staurocytic stomata in *C.* (*Acaules*) *compacta* and their presence in at least one species of *Montiopsis* subg. *Dianthoideae* must not be overlooked when considering function.

In the absence of ultrastructural and/or physiological evidence, the functional significance of trichomes in *Calandrinia* and *Montiopsis* remains conjectural. For example, the multiseriate trichomes composed of intertwined hair cells of *Montiopsis* subg. *Montiopsis*, because of their size, density, and collective wall thickness, might have a protective function (see, e.g., Ehleringer, 1984). The pubescence in most of the species appears sufficiently dense to substantially modify the leaf boundary layer parameters and hence possibly offer protection in the desert and xeric montane habitats where the species occur. When viewed with polarized light, these trichomes produce intricate, colorful diffraction patterns and hence must also modify the quality of solar radiation reaching the photosynthetic tissue. Such speculations on trichome function would require comparative ultrastructural, chemical, and ecophysiological study to verify (e.g., Behnke, 1984; Kelsey et al., 1984).

Foliar venation and stomatal patterning have also been considered on purely developmental grounds (Lyndon, 1990; Meinhardt, 1982; Sachs, 1989, 1991). It has been supposed that the regularity of foliar morphological patterns is a function histogenetic autocatalysis that leads to the development of veins or stomata in one locus and passive or active inhibition of such development in adjacent

loci (Meinhardt, 1982; Sachs, 1989, 1991). Computer simulations of growth in which one or two parameters corresponding to the concentration of physiological regulatory substances are modified have generated intricate patterns such as those characterizing leaf venation (Meinhardt, 1982; Mitchison, 1980).

Emphasizing the inductive effect of auxin on vascular development, Sachs's (1989, 1991) "canalization" hypothesis of vein patterning maintains that, in leaf primordia, the veins are initiated as preferred channels for draining endogenously produced auxin. As the vascular strand develops, its conductive efficiency increases both absolutely and relative to the conductive efficiency of the surrounding cells, which are then passively inhibited from differentiating as vascular tissue. As the leaf expands, and local drainage patterns induce new veins to connect to existing veins, the venation pattern is elaborated. "The difference between vein systems of various leaves would be due to different parameters of auxin formation and transport and to differences in the details of early leaf growth" (Sachs, 1989: 181). Ontogenetic causal mechanisms underlying stomatal complex patterning have also been elaborated (Lyndon, 1990; Meinhardt, 1982; Sachs, 1991).

Developmental models of foliar morphological pattern formation provide the reductionist toe-hold necessary to facilitate experimental analysis, but systematic characterization of patterns, especially when augmented by phylogenetic analysis, provides the phenomena to be explained, a means for assessing the general applicability of a particular model, and a source of natural evolutionary experiments in which developmental differences predicted from models can be studied with the lowest possible degree of interference from evolutionary artifact. The fimbrial vein in *Calandrinia* provides a case in point. Sachs's (1989, 1991) hypothesis implies that vein prominence should be proportional to the importance of the vein for auxin transport during the course of development, and that the auxin source-sink relationship between leaves and roots, respectively, should most strongly influence the attenuation pattern of at least the major veins. It is not obvious why the fimbrial vein in *Calandrinia*—often more prominent than the primary vein in the distal portion of the lamina—should be the preferred channel for auxin drainage. Moreover, the fimbrial vein is exceedingly prominent apically and indistinct basally, i.e., toward the roots. Thus, it might be appropriate to test whether this atypical structure contradicts Sachs's model or is somehow an "exception that proves the rule." The model also predicts that biochemical developmental distinctions should be detectable among the species of *Calandrinia* sect. *Acaules* according to whether or not a fimbrial vein is present in the mature tissue.

An unfortunate aspect of the developmental models is that they appear to uncouple mature tissue structure from mature tissue function. The emphasis on the independence of specific physiological events at different developmental stages is beneficial in dispelling notions of predetermination but may obscure the interdependence of these same events in phylogenetic space. Aspects of the adaptive value of leaf form such as those discussed by Givnish (1979) are undoubtedly significant in determining the survival of a phyletic line. Thus, the role of selection on the mature phenotype as a feedback on the evolution of biochemical ontogeny must be appreciated. Sachs (1991) discussed the potential role of epigenetic selection upon the evolution of pattern formation but emphasized selection during ontogeny rather than selection for functionality after differentiation is completed. Neither the mature foliar morphological patterns, nor ontogenetic studies of relatively few and not closely related species can, by themselves, reveal if and how developmental programs have been rewritten during phyletic evolution. Syntheses of information on developmental mechanisms with knowledge of the diversity of form and phylogenetic reconstructions of the relationships between different forms may thus provide a means through which general theories of development can be advanced and evaluated.

## Conclusions

Foliar morphological evidence corroborates revision of the generic limits of *Calandrinia* and *Montiopsis*. *Calandrinia* is characterized by leaves with a fimbrial vein that overtops and becomes perpendicular to the primary vein at the leaf apex, brachytetracytic/staurocytic stomata commonly with at least a partial outer cycle of subsidiary-like cells, and unicellular ribbed trichomes along the leaf margin. These traits are not universal in *Calandrinia* sect. *Acaules*. Structurally distinct fimbrial veins characterize *Claytonia* and *Montia*, and brachytetracytic stomata characterize one species of the latter. The foliar evidence that *Claytonia* and *Montia* are nested within *Calandrinia* is contradicted by nonfoliar and perhaps additional foliar characters. *Montiopsis* is characterized by its unique trichome types. Only the presence of trichomes per se supports a close relationship between *Calandrinia* and *Montiopsis*. Phylogenetic analysis of foliar characters alone strongly supports a

phylogenetic distinction between the eastern American/African and western American Portulacaceae, with the Australian endemic *Rumicastrum* belonging to the former. The analysis also indicates that foliar characters may be as well conserved evolutionarily as nonfoliar. Existing models relating leaf form to function and ontogeny are generally too rudimentary for reconciliation with the data presented here for *Calandrinia* and *Montiopsis*. Nevertheless, the existence of at least one foliar feature described here, the fimbrial vein in *Calandrinia*, would not appear to have been predicted by current models. The availability of detailed, phylogenetically analyzed systematic accounts of foliar morphology such as that presented here might be exploitable in advancing theories relating mature leaf form to function and development.

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# A REVISION OF *CHIONOLAENA* (COMPOSITAE, GNAPHALIEAE)[1]

*Susana E. Freire*[2]

ABSTRACT

The neotropical genus *Chionolaena* is accepted as including the species of *Leucopholis*, which has been considered a separate genus by several authors because of its few-flowered capitula. *Chionolaena* consists of small, more or less woody shrubs with a discontinuous distribution: central Mexico, northern Colombia, and southern Brazil, with disjunct populations in Central America (Costa Rica) and northern Amazonia (southern Venezuela). The most closely related genus is *Gnaphaliothamnus* from Mexico and Guatemala. Seventeen species of *Chionolaena* are recognized, one of which, *C. mexicana*, is described for the first time. Three new combinations are made: *Chionolaena capitata*, *C. chrysocoma*, and *C. seemannii*. Descriptions, typification, synonymy, distribution maps, illustrations, indices, and a key to all taxa are presented. A cladistic analysis of *Chionolaena* was performed using morphological characters. Polarity of characters was based on outgroup comparison with the genus *Gnaphaliothamnus*. Two monophyletic groups were resolved: (1) the "*concinna* species group" (including *C. concinna* and *C. seemannii*); and (2) the "*mexicana* species group" (including *C. aecidiocephala*, *C. arbuscula*, *C. capitata*, *C. columbiana*, *C. chrysocoma*, *C. eleagnoides*, *C. isabellae*, *C. jeffreyi*, *C. latifolia*, *C. lavandulifolia*, *C. lychnophorioides*, *C. mexicana*, *C. phylicoides*, *C. sartorii*, and *C. wittigiana*). Within each group, this resolution places the Mexican species as the sister group of the South American taxa, i.e., a closer historical relationship is indicated between the Colombian and Brazilian areas than between either and the Mexican area.

*Chionolaena* DC. (including *Leucopholis*) is a genus of small shrubs found in high elevations within the neotropical region (Cabrera & Willink, 1973) from Mexico to southern Brazil. *Chionolaena* comprises 17 species characterized by dichotomously branched stems, reflexed leaves with revolute margins, central florets commonly functionally staminate, and pappus bristles with clavate cells at their tips. It is closely related to the Mexican genus *Gnaphaliothamnus* Kirp.

The last complete taxonomic treatment of this genus was by J. G. Baker (1882), who recognized nine species. Seven species were published by various authors under *Chionolaena* since the appearance of Martius's *Flora Brasiliensis*. In addition to problems with delimitation of species of *Chionolaena*, the generic limits became unclear.

The aims of this revision are to clarify generic and specific limits, to interpret species interrelationships using cladistic methods, and to compare the results of cladistic analysis with the geographic distribution of the genus.

## MATERIALS AND METHODS

This study was based on specimens from the following herbaria: BM, C, COL, E, G, GH, HBG, K, LP, M, MO, NY, P, RB, S, U, UC, US, and W (see List of Exsiccate at end of article). Floral and vegetative parts were dissected and observed after boiling in water. Cross sections of leaves and stems were made by free hand and stained with 2% safranin. All drawings were made by the author from herbarium material.

Information on flowering periods, habitat, and color of corollas was taken from herbarium labels. Species descriptions are presented alphabetically.

The applied cladistics methods were summarized in Nelson & Platnick (1981) and Wiley (1981). Identification of apomorphic characters was based on the outgroup comparison (Platnick, 1979; Watrous & Wheeler, 1981) with *Gnaphaliothamnus* as the outgroup. Table 1 shows the characters and character states used in the cladistic analysis. Five characters have more than two states (4, 6, 8, 9, 10). These characters were treated as nonadditive.

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TABLE 1. Characters and character states.

| Characters | Character states |
|---|---|
| 1. Adaxial leaf surface | tomentose (0); glabrous (1) |
| 2. Leaf margin | slightly revolute (0); conspicuously revolute (1) |
| 3. Stem branching | dichotomous (0); subdichotomous (1) |
| 4. Type of capitulescence | corymbs (0); umbels (a); solitary (b) |
| 5. Corymbophore | absent (0); present (1) |
| 6. Type of capitula | heterogamous (0); homogamous (with perfect florets) (a); nearly unisexual (b); homogamous (with unisexual florets) (c) |
| 7. Inner bracts | obtuse (0); acute (1) |
| 8. Involucre shape | obdeltate (0); narrowly oblong (1 4 mm wide) (a); broadly campanulate (12 mm wide (b) |
| 9. Relation of female to staminate florets in heterogamous capitula | pistillate florets outnumbering the functionally staminate, 5:1 (0); pistillate florets slightly more numerous than functionally staminate florets, 1.1:1–2.5.1 (a); pistillate florets slightly more numerous than functionally staminate or functionally staminate florets slightly more numerous than pistillate (b); functionally staminate florets slightly more numerous than or equaling pistillate, 1:1–2:1 (c) |
| 10. Achene pubescence | shortly pubescent (0); glabrous (a); villous (b) |
| 11. Achenial hairs | obtuse at the tip (0); acute at the tip (1) |
| 12. Pappus bristles | free (0); fused at base into a ring (1) |
| 13. Apical cells of pappus bristles | linear (0); clavate (1) |

In the data matrix (Table 2), plesiomorphic characters were coded with 0, apomorphic ones with 1 (multistate characters with a, b, and c), and unknown characters with question marks. The data matrix was analyzed using the phylogenetic program Hennig86 version 1.5 (Farris, 1988). The options used were "mhennig," for constructing multiple initial cladograms, followed by "bb" (branch breaker). Furthermore, the successive weighting procedure was applied, which calculates weights from the best fits to the most parsimonious trees, using rescaled consistencies (rc), which are the products of the character consistency (c) and the character retention index (r). The product is scaled to lie in the range 0–10. The weighting procedure is repeated on successively produced trees until the trees no longer change (Farris, 1989).

TABLE 2. Data matrix. The character numbers correspond to the numbers used in the text and in the cladograms. Question marks indicate missing information.

| | Character | |
|---|---|---|
| Taxon | 123456789 | 1111 0123 |
| *Gnaphaliothamnus* | 000000000 | 0000 |
| *C. aecidiocephala* | 000a0b100 | 0011 |
| *C. arbuscula* | 100b0blac | b111 |
| *C. capitata* | 000a0blac | b011 |
| *C. columbiana* | 000a1000a | a?11 |
| *C. concinna* | 00100b00b | 0011 |
| *C. chrysocoma* | 110a001aa | a?11 |
| *C. eleagnoides* | 00000000c | a?11 |
| *C. isabellae* | 00001a00? | b111 |
| *C. jeffreyi* | 000b0010c | b011 |
| *C. latifolia* | 100a000ac | b011 |
| *C. lavandulifolia* | 000a0b10b | a?11 |
| *C. lychnophorioides* | 100b001ba | b111 |
| *C. mexicana* | 00000000a | 0011 |
| *C. phylicoides* | 110a0c1a? | b011 |
| *C. sartorii* | 00000010a | 0011 |
| *C. seemannii* | 1010000b0 | 0011 |
| *C. wittigiana* | 10000010c | b111 |

## HISTORICAL SURVEY

*Chionolaena* was first described by de Candolle (1836) on the basis of the Brazilian species *C. arbuscula* from a Vauthier collection. The genus was characterized by its solitary, heterogamous, many-flowered heads in which the central florets were functionally staminate.

In 1843 Gardner created the genus *Leucopholis* on the basis of the Brazilian species *L. phylicoides* with few-flowered, congested, homogamous capitula.

In 1882 Baker placed *Leucopholis* in a section of *Chionolaena*, which is characterized by having capitula with 8–10 florets, in contrast to section *Euchionolaena* with its many-flowered capitula. Six species were listed under section *Euchionolaena*: *C. arbuscula*, *C. lychnophorioides*, *C. gla-*

*ziovii*, *C. glomerata*, *C. isabellae*, and *C. wittigiana*, of which the last four were new. The section *Leucopholis* included three species: *C. latifolia*, *C. phylicoides*, and *C. longifolia*, of which the last was new.

Since 1882, seven species have been added to *Chionolaena*. The first two, *C. eleagnoides* and *C. sartorii*, were described by Klatt (1887: 88) based on Liebman collections from Mexico. The next year, Wawra (1888, 2: 30) described *C. innovans* (presently placed in synonymy of *C. isabellae*). In 1893, B. D. Jackson transferred the Mexican species *Elichrysum lavandulaefolium* Kunth to *Chionolaena*. Blake (1935: 312) described *C. columbiana* from Mexico. It was approximately 50 years before the next species of *Chionolaena*, *C. jeffreyi* H. Robinson (1984: 121) from Brazil and *C. breweri* (Steyermark (1984: 26) (presently placed in synonymy of *C. latifolia*) from Venezuela, were described.

Cabrera (1961) maintained the generic status for *Leucopholis*. He noted that members of this genus are distinguishable by their few-flowered, homogamous heads.

In the present study, *Leucopholis* is not recognized. The species of *Chionolaena* show variation in the number of the flowers and in the proportion of pistillate to functionally staminate florets (including homogamous heads). It is evident that distinction between these genera is impossible based on sexuality alone.

Dillon & Sagástegui (1990) proposed *Pseudoligandra* for the Colombian species *Oligandra chrysocoma* Wedd. According to the cladistic analysis, this new genus cannot be accepted, i.e., *Oligandra chrysocoma* is a derived species with its closest relatives within *Chionolaena*. If *Pseudoligandra* is treated as a separate genus, *Chionolaena* becomes paraphyletic.

## Delimitation and Generic Relationships

*Chionolaena* belongs to Gnaphalieae (sensu Anderberg, 1989; Bremer, 1987) of the Compositae. Merxmüller et al. (1977) considered *Chionolaena* to belong within the "*Lucilia* group" (i.e., *Lucilia*, *Belloa* (= *Lucilia*, Freire, 1986), *Berroa*, *Chevreulia*, *Facelis*, *Gnaphaliothamnus*, *Leucopholis*, *Luciliopsis*, *Mniodes*, and *Raouliopsis*) principally on the basis of its style branches with dorsal sweeping hairs.

*Chionolaena* is distinguished from other genera of Gnaphalieae by its dichotomously branched stems, deflexed leaves (at maturity) with revolute margins, absence of stem phloem fibers, undivided stereome (i.e., lower part uniformly thickened) and white opaque lamina of the inner involucral bracts, often purple upper corollas, functionally staminate hermaphroditic florets, and basally fused pappus bristles with clavate apical cells. *Leucopholis* consistently differs from *Chionolaena* only in having few-flowered capitula. The genus *Leucopholis* is therefore not recognized (see Historical Survey).

Preliminary results from cladistic analysis of Gnaphalieae indicate that *Gnaphaliothamnus* is the sister group of *Chionolaena* (Anderberg, 1989; Anderberg & Freire, 1989). It differs from *Chionolaena* in having free pappus bristles with linear apical cells.

## Morphology

### Habit

The stems are dichotomously branched, i.e., at the apex of each stem there is a terminal aborted primordium or, eventually, a terminal capitulescence. When the capitulescence matures, axillary buds develop, producing a dichotomous growth pattern. In a few species (*C. concinna* and *C. seemannii*), however, only a single bud develops at the base of the capitulescence, and the resulting growth is subdichotomous, leaving the capitulescence conspicuously lateral.

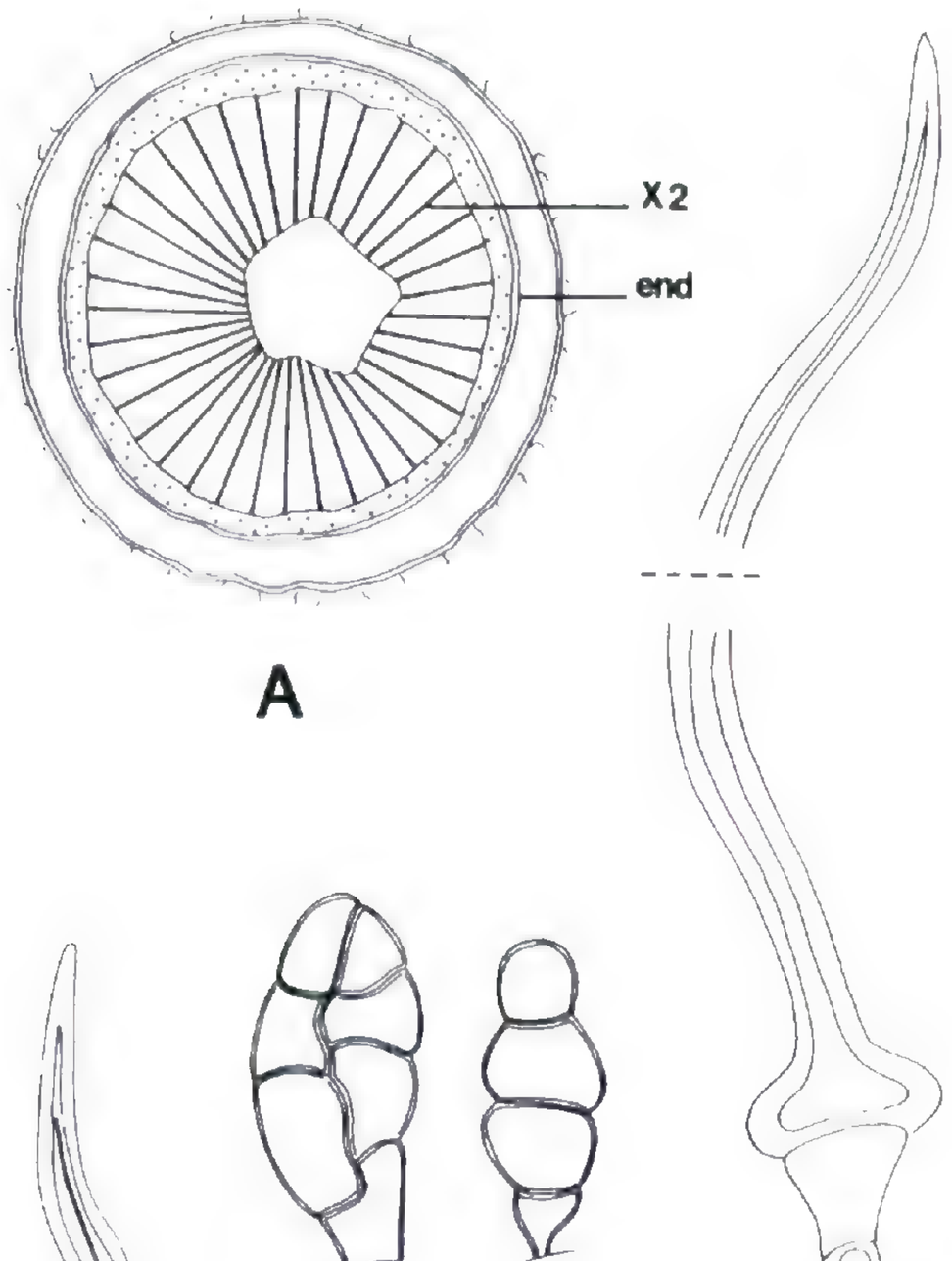
### Trichomes

Throughout *Chionolaena* two types of trichomes occur together on the leaves and stems: nonglandular uniseriate hairs (Fig. 1D) and glandular hairs (Fig. 1C). The former were described as "aseptate flagellate hairs" by Ramayya (1962) and consist of 1–3 small, basal cells and a long, basally swollen terminal cell. Glandular hairs consist of a unicellular basal foot and a uniseriate or biseriate row of cells. Only glandular hairs were found on the abaxial surfaces of corolla apices.

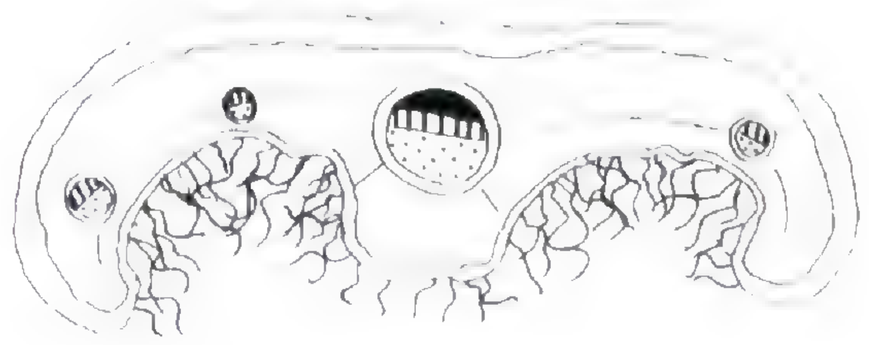
### Capitulescence

The arrangement of the capitula in *Chionolaena* varies (Fig. 1). Heads may be solitary and terminal or densely clustered in umbelliform cymes (i.e., "umbels"). Sometimes these umbelliform clusters are arranged in "corymbs."

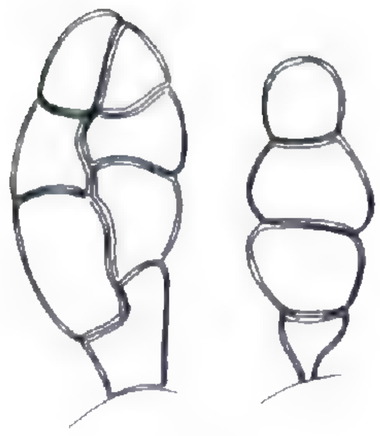
In most species of *Chionolaena* the upper flowering branches are leafy. In some species, e.g., *C. columbiana* and *C. isabellae* (Fig. 1a, b), the capitulescence is supported by a leafless slender stem, i.e., a peduncle, termed "corymbophore" by Lundgren (1972) for *Anaxeton*.



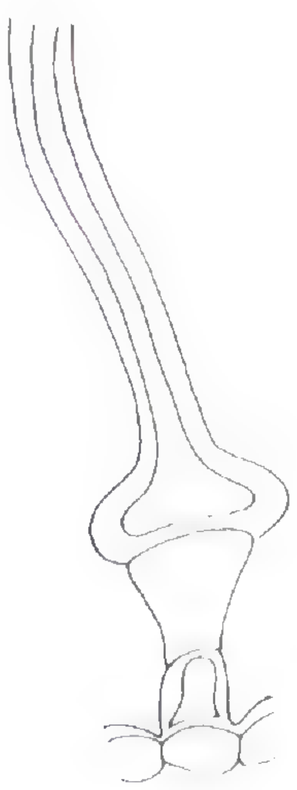

A



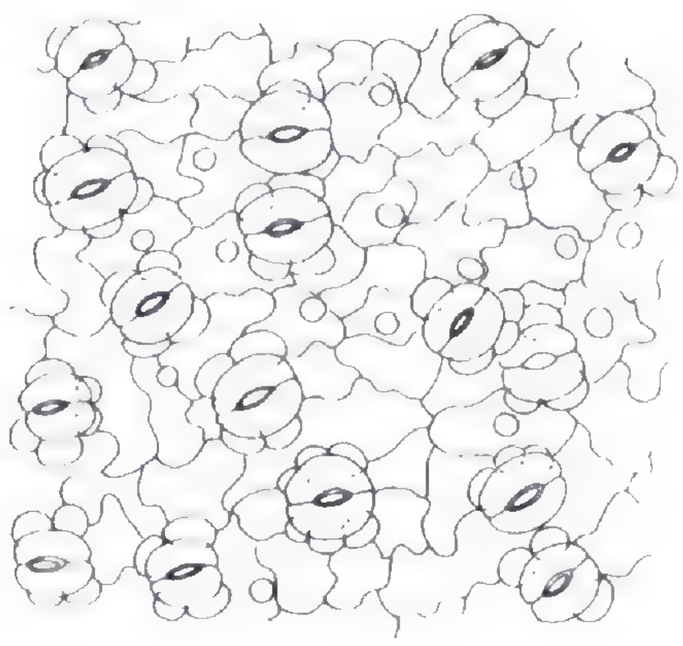
B



C



D



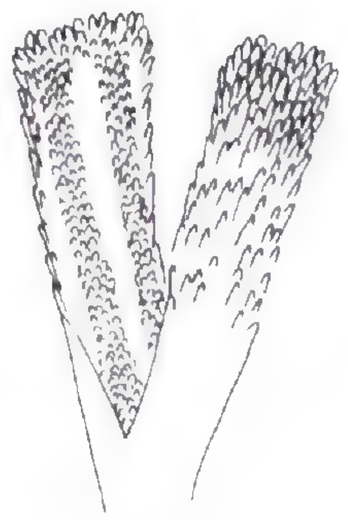
E

F

G

H

I



J

A 1 mm

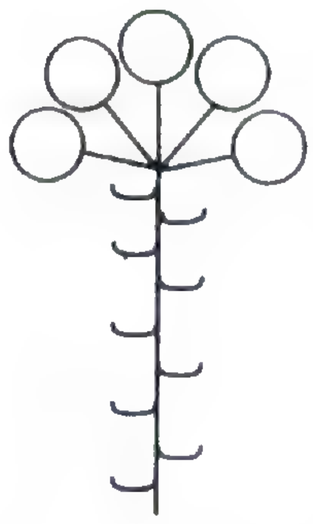
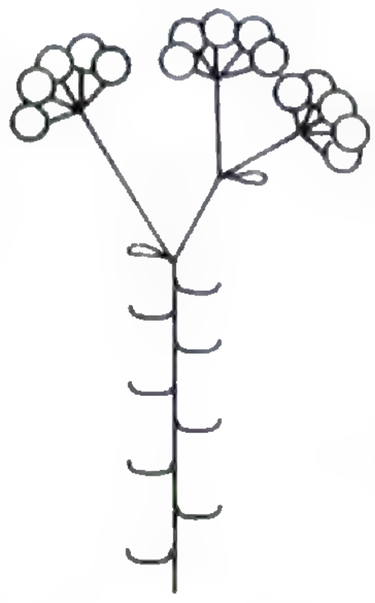
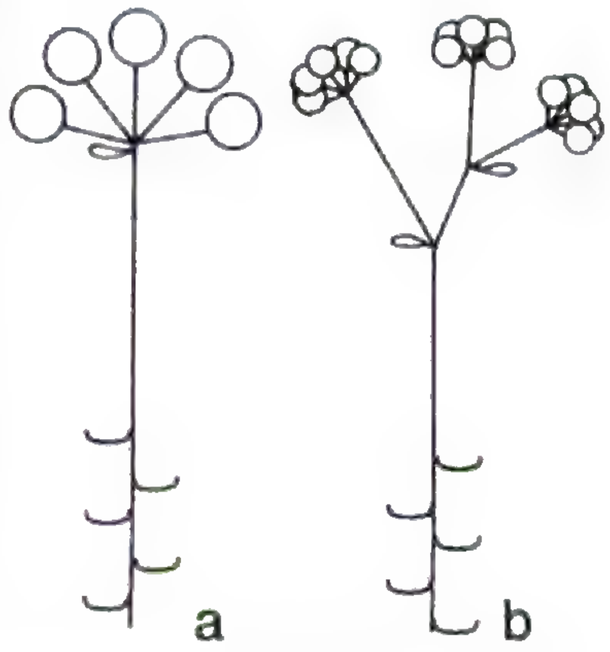
C,D 50 µm

I 0.3 mm

B,H,J 4 mm

E,G 0.1 mm

## CAPITULESCENCE

| solitary | umbel | corymb | with corymbophore |
|---|---|---|---|
| |  |  |  a b |

CAPITULA

The capitula are either heterogamous with functionally staminate florets and pistillate florets, homogamous with perfect florets, or homogamous-unisexual with functionally pistillate or staminate hermaphroditic florets.

The heterogamous condition predominates in *Chionolaena*. Only two species have homogamous capitula: *C. isabellae*, with all perfect florets, and *C. phylicoides*, with unisexual capitula.

Four species of *Chionolaena* are subdioecious: *C. arbuscula*, *C. concinna*, and *C. lavandulifolia* have nearly unisexual capitula in different plants; *Chionolaena aecidiocephala* has two types of capitula, homogamous capitula with all flowers functionally male and heterogamous capitula with pistillate, female flowers as well as male central flowers.

FLORETS

Most species have functionally staminate central florets and filiform, pistillate, peripheral florets. Only one species, *C. aecidiocephala*, shows reduction in the fertility of the staminate florets, i.e., anthers without pollen (neuter florets). All species have fertile pistillate florets.

The proportion of pistillate to functionally staminate florets differs slightly or sometimes markedly. In six species (*C. arbuscula*, *C. capitata*, *C. eleagnoides*, *C. jeffreyi*, *C. latifolia*, and *C. wittigiana*) the functionally staminate florets commonly equal or slightly exceed the pistillate in number (ca. 1 : 1–2 : 1). In other species (*C. chrysocoma*, *C. columbiana*, *C. concinna*, *C. lavandulifolia*, *C. lychnophorioides*, *C. mexicana*, and *C. sartorii*) the pistillate florets are slightly more numerous than the functionally staminate florets (ca. 1.1 : 1–2.5 : 1). In only two species, *C. aecidiocephala* and *C. seemannii*, the female florets outnumber the functionally staminate florets (ca. 5 : 1).

ACHENES

In *Chionolaena* only the pistillate florets are capable of producing achenes, except in *C. isabellae*, which has perfect florets. The sterile ovaries of the functionally staminate florets are usually flattened, without an embryo, and sometimes contracted toward the middle or strongly reduced. Differences between the fertile achene and the sterile ovary are further addressed in the systematic treatment below.

The achenes are usually oblong or oblong elliptic. Within the subdioecious species, only *C. aecidiocephala* has slightly dimorphic achenes, i.e., the central-floret ovary of heterogamous capitula is longer than the central-floret ovary from homogamous capitula.

Within the genus, the achenes may be pubescent or glabrous. *Chionolaena columbiana*, *C. eleagnoides*, *C. chrysocoma*, and, usually, *C. lavandulifolia* have glabrous achenes. The hairs are always 3-cellular, with two parallel elongated cells and a shorter, lateral, basal cell with a thickened outer wall. This "duplex hair" (Hess, 1938) is commonly present in many other genera of the Compositae. In contrast with all other *Chionolaena* species having pubescent achenes, *C. arbuscula*, *C. isabellae*, *C. lychnophorioides*, and *C. wittigiana* have achenial hairs acute at the tip (Fig. 1F). In the remaining species these hairs are obtuse. Furthermore, there is variation in achenial hair length; the four species listed above and *C. phylicoides*, *C. latifolia*, *C. jeffreyi*, and *C. capitata* have sericeous, villous achenes with hairs ca. 0.3 mm long, whereas *C. aecidiocephala*, *C. lavandulifolia* (when hairy), *C. seemannii*, and *C. sartorii* have hairs ca. 0.1 mm long (Fig. 1G).

CHROMOSOME NUMBER

Gametic chromosome number has been investigated in one species of *Chionolaena*, i.e., *C. la-*

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FIGURE 1. *Chionolaena*. —A. *C. aecidiocephala*, cross section of stem with continuous secondary xylem (X2) and differentiated endodermis (end).—B. *C. arbuscula*, cross section of leaf with revolute margins densely lanate on the abaxial face. C, D. *C. isabellae*, leaf hairs. C. Glandular hairs biseriate type.—D. Aseptate flagellate hair with apical cell swollen at the base.—E. *C. latifolia*, abaxial epidermis with cyclocytic stomata. F, G. Achene hairs.—F. *C. isabellae*, elongated tricellular hair with acute tip.—G. Short, clavate hair with obtuse tip.—H. *C. aecidiocephala*, pappus bristles fused together near the base forming a single ring below.—I. *C. eleagnoides*, pappus bristles with clavate apical cells.—J. *C. wittigiana*, style branches with two parallel stigmatic areas on the abaxial surface and with sweeping hairs on the adaxial side. A, G, H, *MacDougall 4129* (S); B, *Irwin et al. 29023* (NY); C, *Glaziou 6601* (S); D, *Cabrera 25329* (LP); E, *Hemmendorff 648* (S); F, *Cuchioni 940* (LP); I, *Liebman 316* (GH); J, *Dusén E132* (S). Diagrams of capitulescence types in *Chionolaena*: solitary (*C. arbuscula*, *C. jeffreyi*, *C. lychnophorioides*); umbel (*C. aecidiocephala*, *C. capitata*, *C. chrysocoma*, *C. latifolia*, *C. lavandulifolium*, *C. phylicoides*); corymb (*C. concinna*, *C. eleagnoides*, *C. mexicana*, *C. sartorii*, *C. seemannii*, *C. wittigiana*); capitulescence supported by corymbophore (a, *C. columbiana*; b, *C. isabellae*).

*vandulifolia* (= *Gnaphalium lavandulifolium*), which was found to have $n = 14$ by De Jong & Longpre (1963). This number suggests tetraploidy, based on $x = 7$ in Gnaphaliinae (Merxmüller et al., 1977).

## Cladistics

*Chionolaena* and its sister group, *Gnaphaliothamnus*, form a larger monophyletic group that is characterized by having dichotomously branched stems without phloem fibers, reflexed leaves (at maturity) with revolute margins, an undivided stereome in the inner bracts, and commonly functionally staminate central florets. *Chionolaena* is morphologically distinct because its pappus bristles are fused at the base into a ring and have clavate cells at their tips.

Thirteen apomorphic character states were found (Table 1) by outgroup comparison (Hennig, 1966; Platnick, 1979; Watrous & Wheeler, 1981) using the monotypic genus *Gnaphaliothamnus* as outgroup. Thirty-five equally parsimonious cladograms were generated from the data matrix. All have 39 steps, a consistency index of 0.51, and a retention index of 0.62. If the synapomorphies for the whole genus (characters 12 and 13) are excluded, the consistency index is 0.48. When the successive weighting procedure was applied, 11 minimum length trees resulted after the second round of weighting, with length 118, a consistency index of 0.68, and a retention index of 0.75. Again, if the synapomorphies for the whole genus are ignored, the consistency index is 0.62.

The strict consensus tree of the 11 cladograms (Fig. 2) shows that there are three monophyletic groups: (1) the "*concinna* species group" (including *C. concinna* and *C. seemannii*); (2) the "*eleagnoides* species group" (including *C. eleagnoides*, *C. columbiana*, and *C. isabellae*) and (3) the "*sartorii* species group" (including *C. sartorii*, *C. lavandulifolia*, *C. aecidiocephala*, *C. jeffreyi*, *C. capitata*, *C. wittigiana*, *C. lychnophorioides*, *C. arbuscula*, *C. latifolia*, *C. chrysocoma*, and *C. phylicoides*). *Chionolaena mexicana* appears to be isolated.

As an example of how characters may be distributed, I have presented one of the 11 equally parsimonious cladograms (Fig. 3). The cladogram chosen shows two monophyletic groups: (1) the "*concinna* species group" (including *C. concinna* and *C. seemannii*) and (2) the "*mexicana* species group" (including *C. mexicana*, *C. eleagnoides*, *C. columbiana*, *C. isabellae* *C. sartorii*, *C. lavandulifolia*, *C. aecidiocephala*, *C. jeffreyi*, *C. capitata*, *C. latifolia*, *C. chrysocoma*, *C. phylicoides*, *C. wittigiana*, *C. arbuscula*, and *C. lychnophorioides*).

The Mexican species *C. concinna* and *C. seemannii* have stems subdichotomously branched (character 3). Fifteen species comprise the "*mexicana* species group," which is defined by the slightly more numerous pistillate florets than functionally staminate florets (character 9a). Two species groupings appear within this last group: the "*eleagnoides* species group" (including *C. eleagnoides*, *C. columbiana*, and *C. isabellae*") and the "*sartorii* species group" (including *C. sartorii*, *C. lavandulifolia*, *C. aecidiocephala*, *C. jeffreyi*, *C. capitata*, *C. latifolia*, *C. chrysocoma*, *C. phylicoides*, *C. wittigiana*, *C. arbuscula*, and *C. lychnophorioides*). *Chionolaena eleagnoides* from Mexico, *C. columbiana* from Colombia, and *C. isabellae* from Brazil have glabrous achenes (character 10a). *Chionolaena columbiana* and *C. isabellae* appear together united by capitula supported by a corymbophore (character 5). The second large monophyletic group, "*sartorii* species group," is justified by the acute inner bracts (character 7). *Chionolaena sartorii* is the sister species of the other "*sartori* group" taxa. The latter species are united by umbelliform clusters of capitula (character 4a). There are two monophyletic groups within the last group. The Mexican species *C. lavandulifolia* and *C. aecidiocephala* share capitula nearly unisexual (character 6b). The second monophyletic group is formed by the mostly Brazilian species *C. jeffreyi*, *C. capitata*, *C. latifolia*, *C. chrysocoma*, *C. phylicoides* *C. wittigiana*, *C. arbuscula*, and *C. lychnophorioides*. They are united by villous achenes (character 10b) and the functionally staminate florets slightly more numerous than or equaling pistillate florets (character 9c). The relationships among *C. capitata*, *C. jeffreyi*, and *C. latifolia* are unclear. *Chionolaena arbuscula* and *C. lychnophorioides* appear together united by the solitary capitula (character 4b). In some solutions, *C. arbuscula* and *C. wittigiana* appear together, whereas in other solutions *C. arbuscula* is placed as the sister species of *C. lychnophorioides* and *C. wittigiana*. *Chionolaena wittigiana*, *C. arbuscula*, and *C. lychnophoriodes* have achenial hairs acute at the tip (character 11). In all cases *C. chrysocoma* and *C. phylicoides* appear together, sharing conspicuously revolute leaf margins (character 2).

The sections distinguished by Baker (1882), section *Euchionolaena* (*C. arbuscula*, *C. isabellae*,

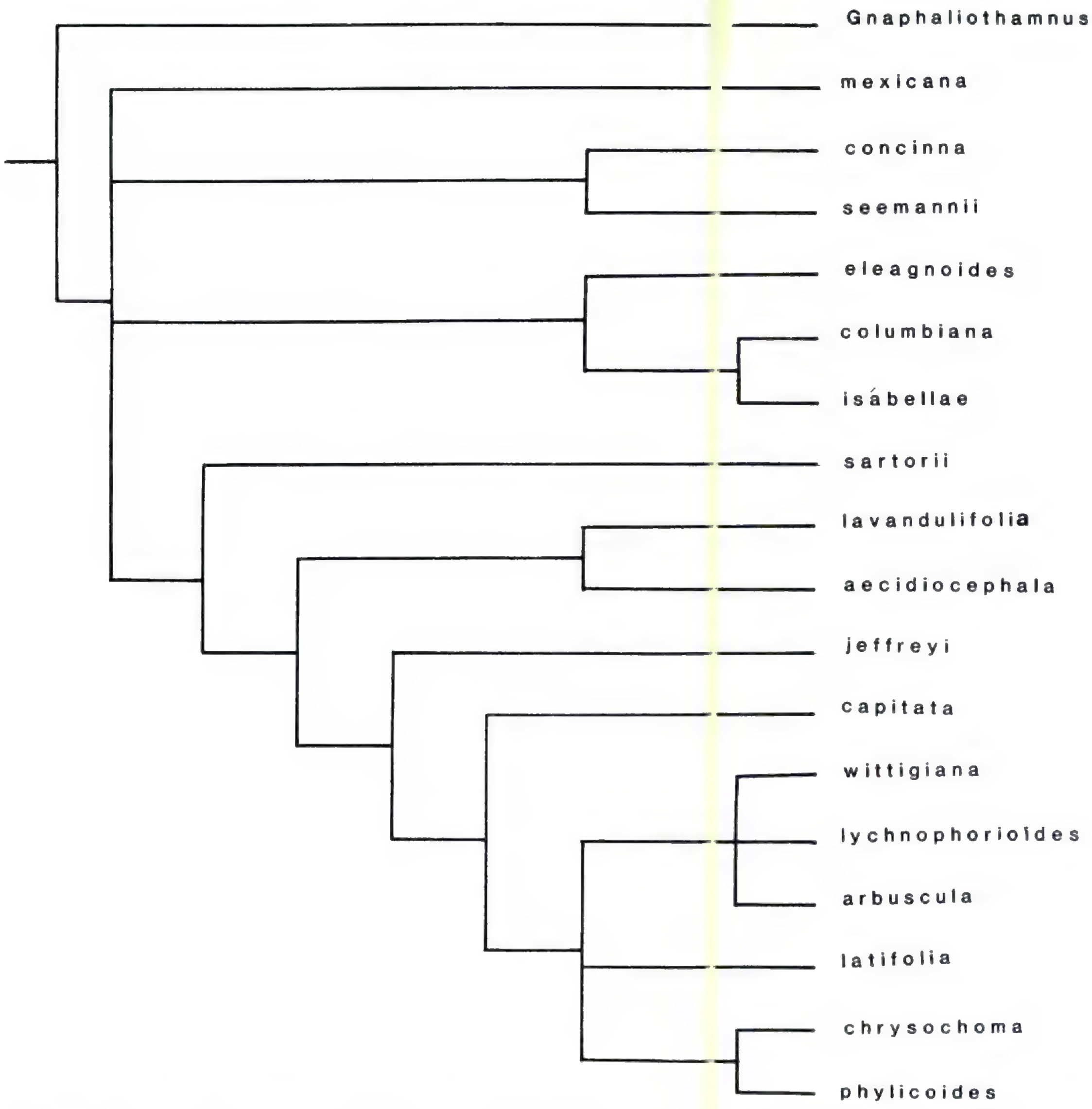



FIGURE 2. The strict consensus tree of relationships among species of *Chionolaena* for all equally parsimonious trees.

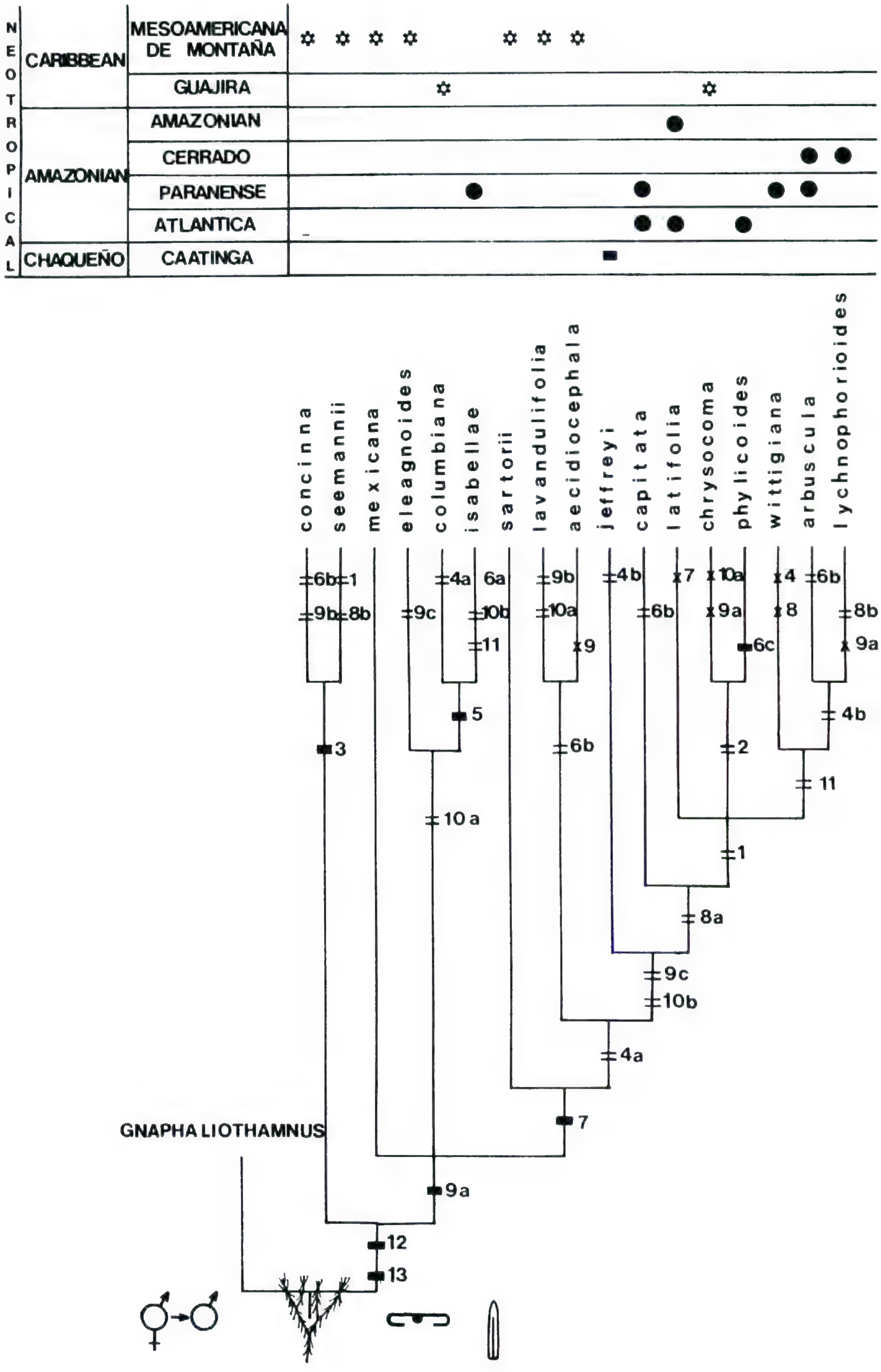
*C. lychnophorioides, C. wittigiana*) and section *Leucopholis* (*C. phylicoides, C. latifolia*) do not represent monophyletic groups. The character by which these sections have been separated (number of florets per capitulum) is variable intragenerically and also sometimes infraspecifically.

## BIOGEOGRAPHY

The total range of *Chionolaena* (Fig. 4A) comprises the montane habitats of America within the neotropical region (Caribbean, Amazonian, and Chaqueño dominions) as distinguished by Cabrera & Willink (1973).

*Chionolaena* has a discontinuous distribution; it is present in central Mexico, Central America (Costa Rica), northern Colombia, southern Brazil, and northern Amazonia (southern Venezuela). Plant species with similar ranges are frequent, e.g., *Agarista* (Judd, 1984), *Heliconia* (Andersson, 1985), *Maranta* (Andersson, 1986), and ferns (Tryon, 1962, 1970; Conant, 1983). The floristic relationships among the highlands of Mexico and Amazonas and the Andean region have been expressed by Hemsley (1879–1880, vol. 4: 228) and Epling (1940) in Rzedowski (1965).

The monotypic *Gnaphaliothamnus*, the sister


NEOTROPICAL
CARIBBEAN
MESOAMERICANA DE MONTAÑA
GUAJIRA
AMAZONIAN
AMAZONIAN
CERRADO
PARANENSE
ATLANTICA
CHAQUEÑO
CAATINGA
concinna
seemannii
mexicana
eleagnoides
columbiana
isabellae
sartorii
lavandulifolia
aeecidiocephala
jeffreyi
capitata
latifolia
chrysocoma
phylicoides
wittigiana
arbuscula
lychnophorioides
GNAPHA LIOTHAMNUS

group of *Chionolaena*, has a Mexican and Central American (Guatemala) distribution.

The 17 species of *Chionolaena* are distributed as follows, according to Cabrera & Willink (1973): seven species (*C. aecidiocephala*, *C. concinna*, *C. eleagnoides*, *C. lavandulifolia*, *C. mexicana*, *C. sartorii*, and *C. seemannii*) are narrowly endemic to the mountainous areas of central Mexico (most being known from a single locality) in the "Mesoamerican Mountain" Province within the Caribbean Dominion. *Chionolaena lavandulifolia* has disjunct populations in central Costa Rica as well. Two species (*C. columbiana* and *C. chrysocoma*) are confined to the northern Andes of Colombia, on the Sierra de Santa Marta and the Sierra de Perijá, in the "Guajira" Province within the Caribbean Dominion. The remaining species are endemic to the mountains of southern Brazil in the Chaqueño Dominion ("Caatinga" Province: *C. jeffreyi*) and Amazonian Dominion ("Amazonian" Province: *C. latifolia*; "Cerrado" Province: *C. arbuscula* and *C. lychnophorioides*; "Paranense" Province: *C. isabellae*, *C. capitata*, *C. wittigiana*, and *C. arbuscula*; "Atlantica" Province: *C. capitata*, *C. latifolia*, *C. phyllicoiodes*). Only *C. latifolia* has a disjunct distribution, being also recorded from Cerro Marahuaca in Venezuelan Guayana.

In order to formulate biogeographic hypotheses for the central Mexican, Colombian Andean, and southern Brazilian areas in the neotropical region, cladistic analysis of *Chionolaena* was used. Additional cladistic analyses of other taxa in this region will allow testing the following results.

In the area cladograms (Fig. 4B, C) based on the consensus tree (Fig. 2), the name of each taxon was replaced by an abbreviation of the area in which it occurs. The first events leading to the separation of the ancestral population of *Chionolaena* are unclear. The three monophyletic groups, the "*concinna* species group," the "*eleagnoides* species group," and the "*sartorii* species group," identified in the consensus tree (Fig. 2) can, however, be used to analyze the relationships between the geographical areas of each taxon. Two of these groups, the "*eleagnoides* species group" and the "*sartorii* species group" are today sympatric and present similar vicariant patterns, which can be presumed to have developed simultaneously.

In the "*eleagnoides* species group," two principal vicariant events can be postulated. The first event could have split a large and continuous population into northern (evolving into a Mexican taxon, i.e., *C. eleagnoides*) and southern (evolving into South American taxa) populations. The second event could have separated a small population in the Colombian area (evolving into *C. columbiana*) from the more southern population, which evolved into the Brazilian taxon (*C. isabellae*) (Fig. 4D).

In the "*sartorii* species group," a Mexican population (evolving into *C. sartorii*, *C. lavandulifolia*, and *C. aecidiocephala*) may have first split off from the main population. Subsequently, a large Brazilian population (evolving into *C. jeffreyi*, *C. capitata*, *C. latifolia*, *C. wittigiana*, *C. arbuscula*, and *C. lychnophorioides*) could have become isolated from the rest of the main population. The remaining population may have then extended its range toward the southeast and split off another Brazilian population (evolving into *C. phylicoides*) leaving behind a Colombian population (evolving into *C. chrysocoma*).

To summarize, although the sequential events involved in this group are unclear because the phylogeny is unresolved, it is clear that a closer biogeographical relationship exists between the Colombian Andean and southern Brazilian areas than between either and the central Mexican area.

## Systematic Treatment

*CHIONOLAENA*

**Chionolaena** DC., Prodr. 5: 397. 1836. TYPE: *Chionolaena arbuscula* DC.

*Leucopholis* Gardner, London J. Bot. 2: 10. 1843. TYPE: *Leucopholis phylicoides* Gardner.

*Pseudoligandra* Dillon & Sagást., Taxon 39: 125. 1990. TYPE: *Pseudoligandra chrysocoma* (Wedd.) Dillon & Sagást.

Shrubs or subshrubs. Stems erect or ascendent, dichotomously or subdichotomously branched, woolly tomentose and leafy when young but later glabrous and leafless with marked leaf scars in the lower parts. Vascular cylinder without phloem fibers, surrounded by a distinct endodermis (Fig. 1A). *Leaves* sessile, closely set or spreading, sub-

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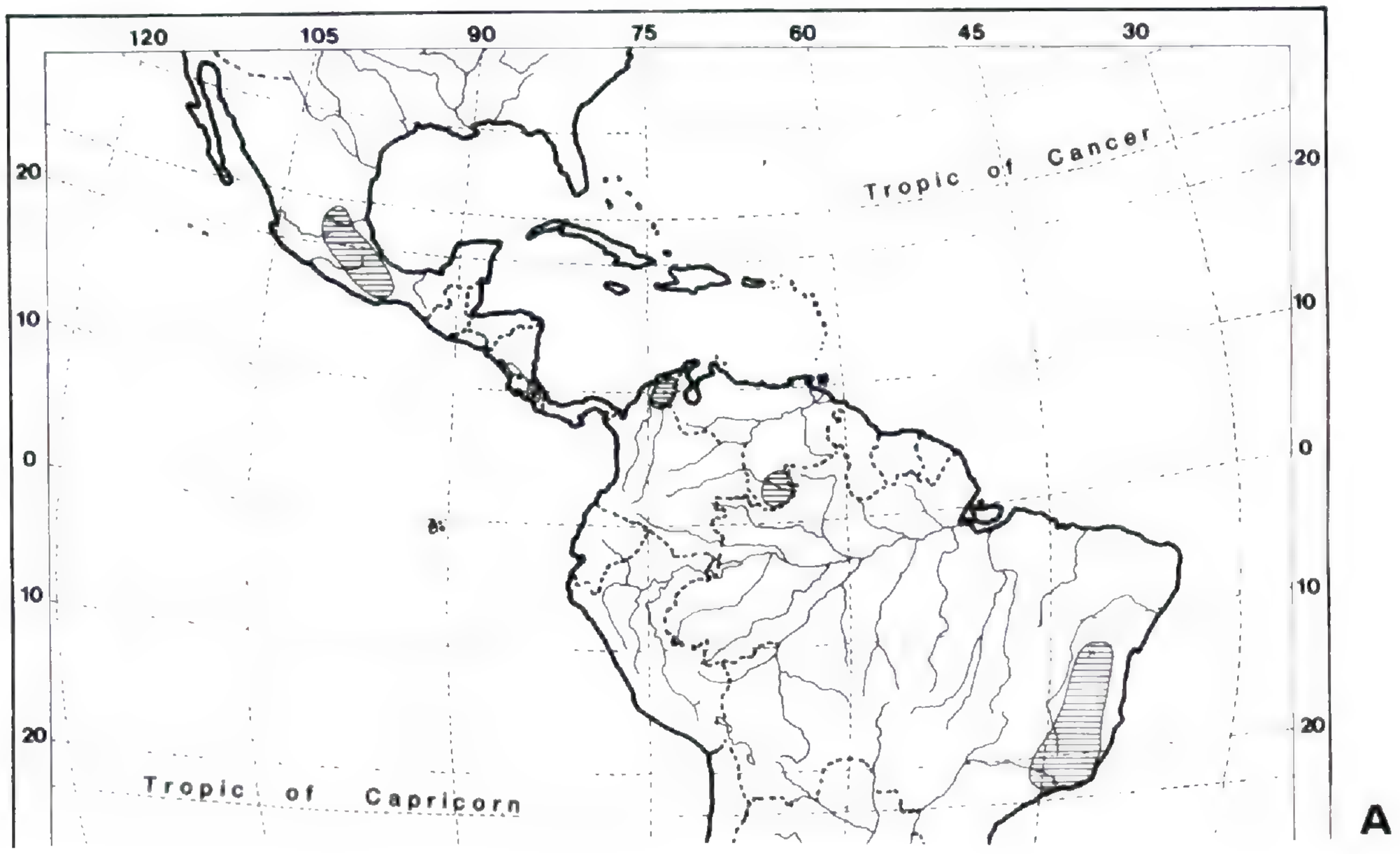
FIGURE 3. One of the 16 equally parsimonious cladograms, illustrating character distribution. Black bars indicate synapomorphies, "X" indicates apparent reversals of a character state, "=" indicates parallelism. Numbers refer to characters listed in Table 1. Geographic distributions are summarized by biogeographic regions, dominions, and provinces as outlined in Cabrera & Willink (1973).


120
105
90
75
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45
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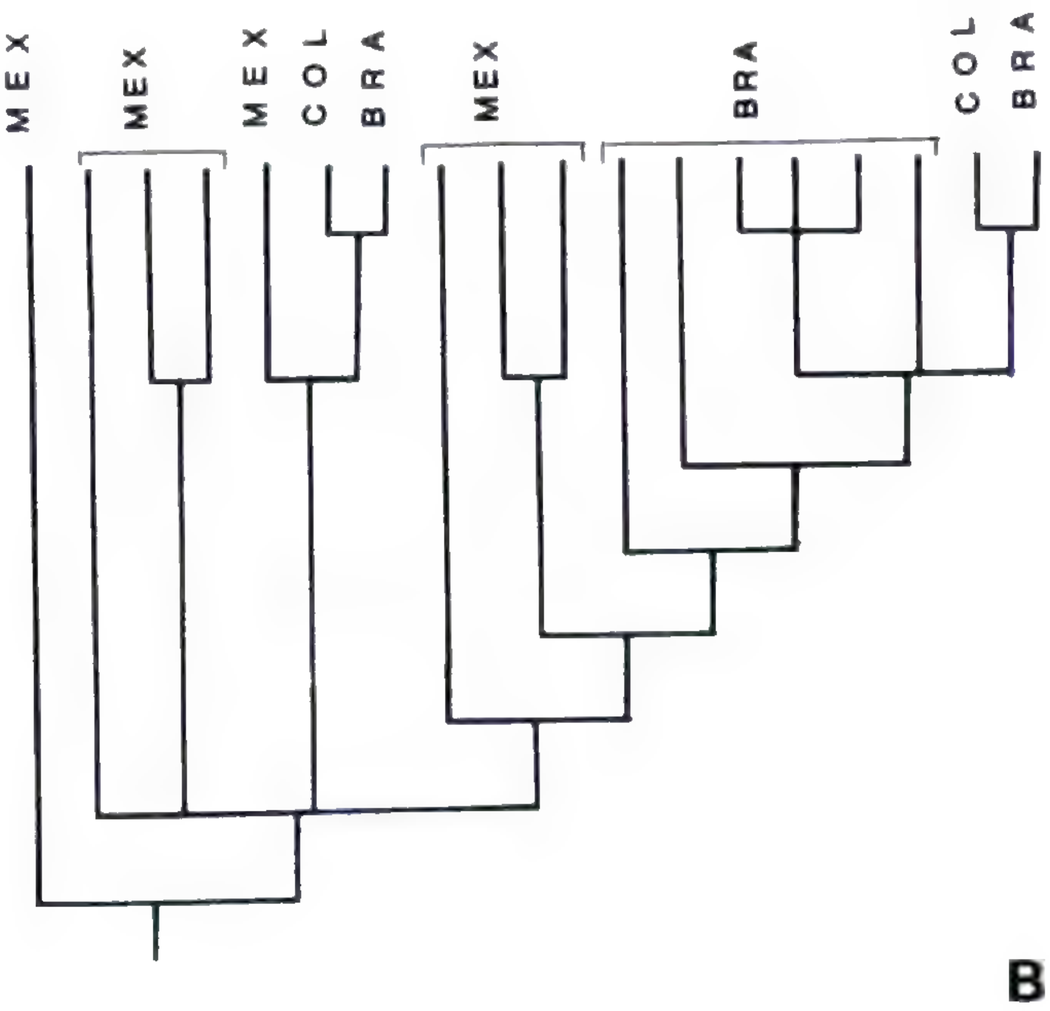
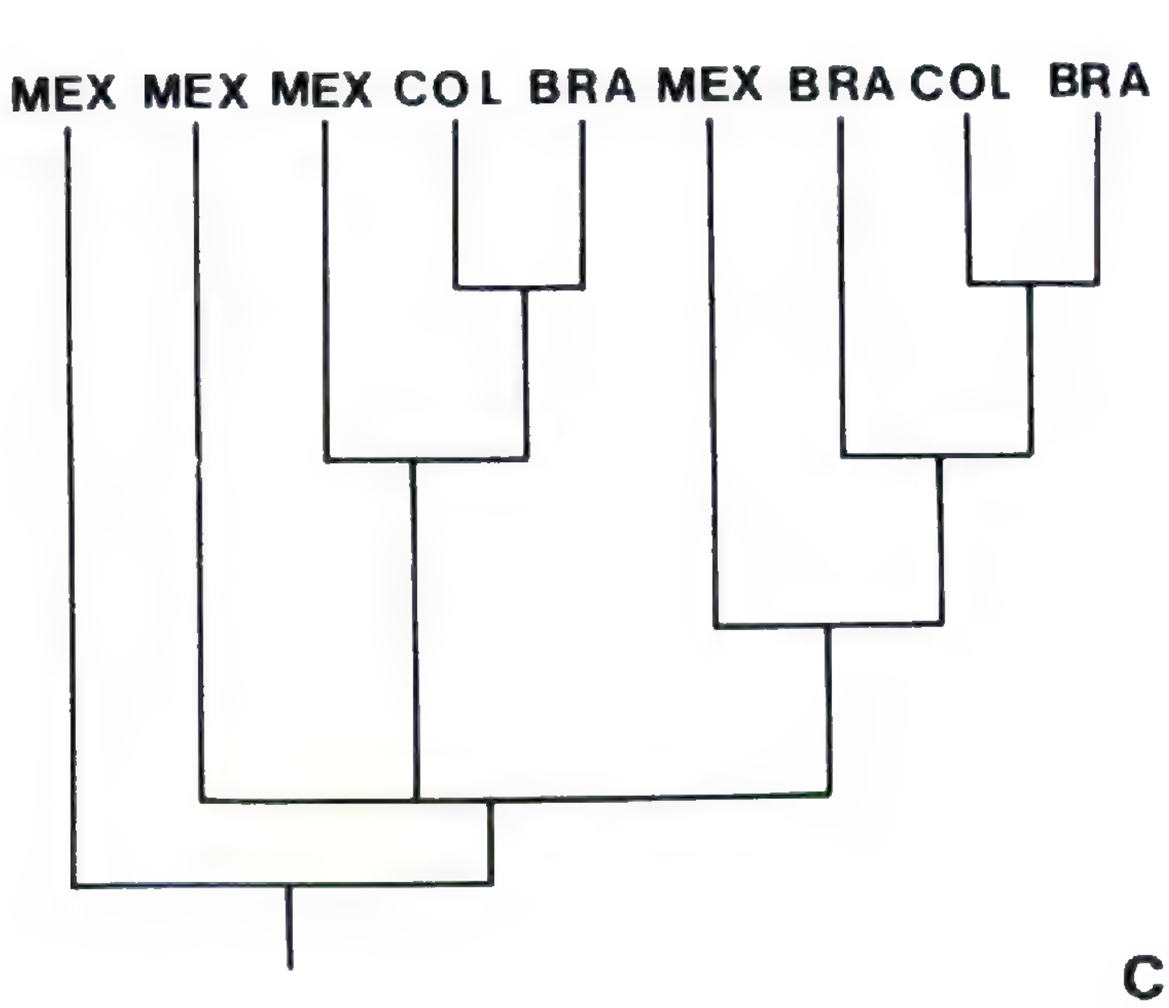
0
10
20
Tropic of Cancer
Tropic of Capricorn

A



B


MEX MEX MEX COL BRA MEX BRA COL BRA

C

MEX
COL
BRA

D

decussate, in four distinct rows; erect in the upper part of the stem, becoming reflexed with age (only one species has appressed leaves); midrib prominent; margins entire, slightly or conspicuously revolute (Fig. 1B); mucronate; adaxially glabrous or tomentose, abaxially densely lanate and whitish, with glandular and nonglandular hairs (Fig. 1C, D). Epidermis with cyclocitic stomata surrounded by 4–6 subsidiary cells scattered on the abaxial surface (Fig. 1E); cuticle thick. *Capitula* shortly pedunculate in dense umbels or corymbose capitulescences, sometimes solitary, terminal on the main stems, sometimes supported by a slender peduncle (Fig. 1). Heterogamous or homogamous. *Involucres* narrowly oblong, campanulate or broadly campanulate; bracts imbricate, membranaceous, generally yellowish brown, entire; outer ones broadly ovate to linear-ovate, acute, obtuse or acuminate at the apex, pubescent adaxially; innermost bracts narrow, linear or obovate, obtuse or acute at the apex, glabrous with white opaque lamina and lower part uniformly thickened (i.e., stereome undivided). *Receptacle* glabrous, flat or somewhat convex, epaleate. *Florets* 5 to ca. 100; corollas white-cream, often red-tipped; pistillate florets (when present) fewer than, equaling, or more numerous than the hermaphroditic ones. *Pistillate florets* fertile; corollas filiform, minutely bilabiate, lobes with biseriate glandular hairs. Styles bifid; style branches erect to spreading, linear, glabrous, rounded; stylopodium indistinct. *Achenes* narrowly oblong or narrowly elliptic, glabrous or pubescent with long or short duplex hairs (Fig. 1F, G). *Pappus* bristles as in hermaphroditic florets but with apical cells slightly inflated, not clavate. *Hermaphroditic florets* functionally staminate (occasionally functionally pistillate, neuter, or fully fertile); corollas tubular, slightly expanded at top, 5-lobed, the lobes papillose with biseriate glandular hairs. Styles shortly bifid or sometimes undivided; the branches rounded truncate or acute; with apically obtuse sweeping hairs, commonly the sweeping hairs occurring almost to the stylar partition; abaxial faces with two parallel stigmatic areas constituted by small and rounded papillae (Fig. 1J); stylopodium and stylophore (between the ovary and the stylopodium) developed. *Anthers* 5, caudate, with ovate apical appendages, thickenings in endothecial tissue, antheropodium (collar) distinct, tails slightly shorter than, equaling, or longer than the antheropodium. *Ovaries* flattened, often strongly contracted with embryo not developed. *Pappus* bristles ± thick, barbellate with clavate (occasionally slightly inflated) apical cells (Fig. 1I); fused at the base into a single ring and connate in groups of different lengths (Fig. 1H); equaling the corolla.

The name of the genus seems to refer to the snow white and cottony tomentum on the lower surface of the leaves (from Greek, "chionos" = snow, "laenos" = cloak or mantle).

*Distribution.* Seven species from the central region of Mexico; two species confined to the northern area of Colombia; and eight species in southern Brazil.

*Local name.* The name "Arnica" is applied to some Brazilian species (Glaziou, 1910), viz, *C. arbuscula* var. *hololeuca* (= *C. capitata*), *C. innovans* (= *C. isabellae*), *C. wittigiana*, and *C. glomerata* (= *C. latifolia*).

KEY TO THE SPECIES OF *CHIONOLAENA*

1a. Capitula solitary (occasionally arranged in terminal, small, loose umbels).
  2a. Subshrub with ascending stems; leaves with lamina conspicuously narrowed at the base; achene hairs obtuse at the apex ..... 9. *C. jeffreyi*
  2b. Shrubs erect, rigid, woody; leaves not notably narrowed at the base; achene hairs acute at the apex.
    3a. Leaves narrowly linear, 0.7–1 mm wide, margins conspicuously revolute ..... 2. *C. arbuscula*
    3b. Leaves broadly linear, 1.2–3 mm wide, margins slightly revolute ..... 12. *C. lychnophorioides*
1b. Capitula arranged in clusters or corymbs.
  4a. Capitula arranged in dense umbels.
    5a. Umbels supported by a peduncle at maturity ..... 4. *C. columbiana*
    5b. Umbels sessile at maturity.
      6a. Involucres narrowly oblong.
        7a. Leaves with lower lamina completely concealed by the revolute margins.

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FIGURE 4.—A. Distribution of *Chionolaena*. B,C. Area cladograms.—B. Complete area cladogram with the same topology as the consensus tree in Figure 2. (Names of taxa were substituted by abbreviations of geographical areas.)—C. Reduced area cladogram. Groups of taxa occurring in the same area were reduced to a single branch in the cladogram.—D. Postulated distribution of the ancestral population after the two principal vicariant events. (MEX = Mexican area, COL = Colombian area, BRA = Brazilian area.)

8a. Leaves reflexed; achenes pubescent; capitula homogamous (unisexual) ..... 14. *C. phylicoides*
8b. Leaves closely appressed to stem; achenes glabrous; capitula heterogamous ..... 6. *C. chrysocoma*
7b. Leaves with lower surface visible (leaf margins slightly revolute).
9a. Leaves elliptic, 1.5–4 cm long, adaxial face glabrous ..... 10. *C. latifolia*
9b. Leaves linear, 5–13 mm long, adaxial face tomentose ..... 3. *C. capitata*
6b. Involucres obdeltate.
10a. Erect, rigid shrub; leaves suborbicular ..... 1. *C. aecidiocephala*
10b. Caespitose shrub; leaves linear-elliptic ..... 11. *C. lavandulifolia*
4b. Capitula arranged in corymbs.
11a. Leaves broadly obovate, 11–12 mm wide; achenes glabrous ..... 7. *C. eleagnoides*
11b. Leaves obovate, linear, or elliptic (when obovate 3–7 mm wide); achenes pubescent.
12a. Achenes sericeous; achene hairs acute or subacute.
13a. Leaves narrowly obovate; corymbs lax, supported by a peduncle at maturity ..... 8. *C. isabellae*
13b. Leaves linear; corymbs dense, sessile ..... 17. *C. wittigiana*
12b. Achenes with short obtuse hairs.
14a. Leaves linear to elliptic.
15a. Subshrub weakly woody, caespitose; leaves narrowly linear, 1–2 cm long, 1 mm wide; corymbs of 3–4 capitula ..... 15. *C. sartorii*
15b. Shrub woody, rigid, ascendent; leaves linear-elliptic, 3.5–4.5 cm long, 4–5 mm wide; corymbs of many capitula (up to 10) ..... 16. *C. seemannii*
14b. Leaves obovate.
16a. Dichotomously branched, rigid shrub; capitulescence terminal at maturity; leaves slightly attenuate at the base ..... 13. *C. mexicana*
16b. Subdichotomously branched subshrub; capitulescence lateral at maturity; leaves subpetiolate ..... 5. *C. concinna*

**1. Chionolaena aecidiocephala** (Grierson) Anderberg & Freire, Notes Roy. Bot. Gard. Edinburgh 46(1): 37–41. 1989. *Anaphalis aecidiocephala* Grierson, Notes Roy. Bot. Gard. Edinburgh 31: 389, fig. 1972. *Gnaphalium aecidiocephalum* (Grierson) L. O. Williams., Phytologia 25: 459. 1973. TYPE: Mexico. Oaxaca: Ixtlán, Comaltepec, Cerro de Humo Chico, in grass in sun, 3,050 m, 2 Mar. 1968, *MacDougall 4129* (holotype, E; isotype, S). Figure 5.

Erect, multibranched, rigid shrub, 10–20 cm high. *Leaves* suborbicular, obtuse, 2.5–5 mm long, 1.5–3 mm wide with slightly revolute margins, tomentose adaxially, densely whitish lanate abaxially. *Capitula* homogamous and heterogamous, arranged in dense umbels sessile and terminal on the upper branches. *Involucre* obdeltate. Involucral bracts ca. 32; outer bracts ovate, obtuse, 3–4 mm long, 2–2.5 mm wide, purple at the tip; inner bracts linear, slightly obtuse, 6–8 mm long, 0.8–1.2 mm wide, purplish above stereome. *Florets* 29–35, pistillate florets more numerous than the functionally staminate or all functionally staminate in homogamous capitula. *Pistillate florets* (0–)25–26; corollas 4 mm long; achenes elliptic, 1–1.5 mm long, 0.25–0.40 mm wide, pubescent with short, apically obtuse, duplex hairs. *Functionally staminate florets* 5 (and functionally neuter in heterogamous capitula), 29–35 (in homogamous capitula); corollas 3.5–4 mm long; style branches rounded, 0.2 mm long; fertile anthers 2 mm long with tails slightly shorter than antheropodium; sterile anthers 1.5 mm long, tails slightly exceeding antheropodium and without pollen grains; ovaries sterile, flattened, 0.5–0.8 mm long, 0.25–0.30 mm wide, shortly pubescent as in pistillate florets.

*Distribution.* Known only from the type locality, i.e., mountains of Oaxaca in Mexico, growing between 2,700 and 3,050 m. Flowering collection was made in March.

*Additional specimen examined.* MEXICO. OAXACA: Ixtlán, Comaltepec, in grass in sun, Cerro de Humo Chico, 10,000 ft., *T. MacDougall*, 6 Jan. 1961 (E).

*Chionolaena aecidiocephala* is distinguished from other Mexican species of the genus by its

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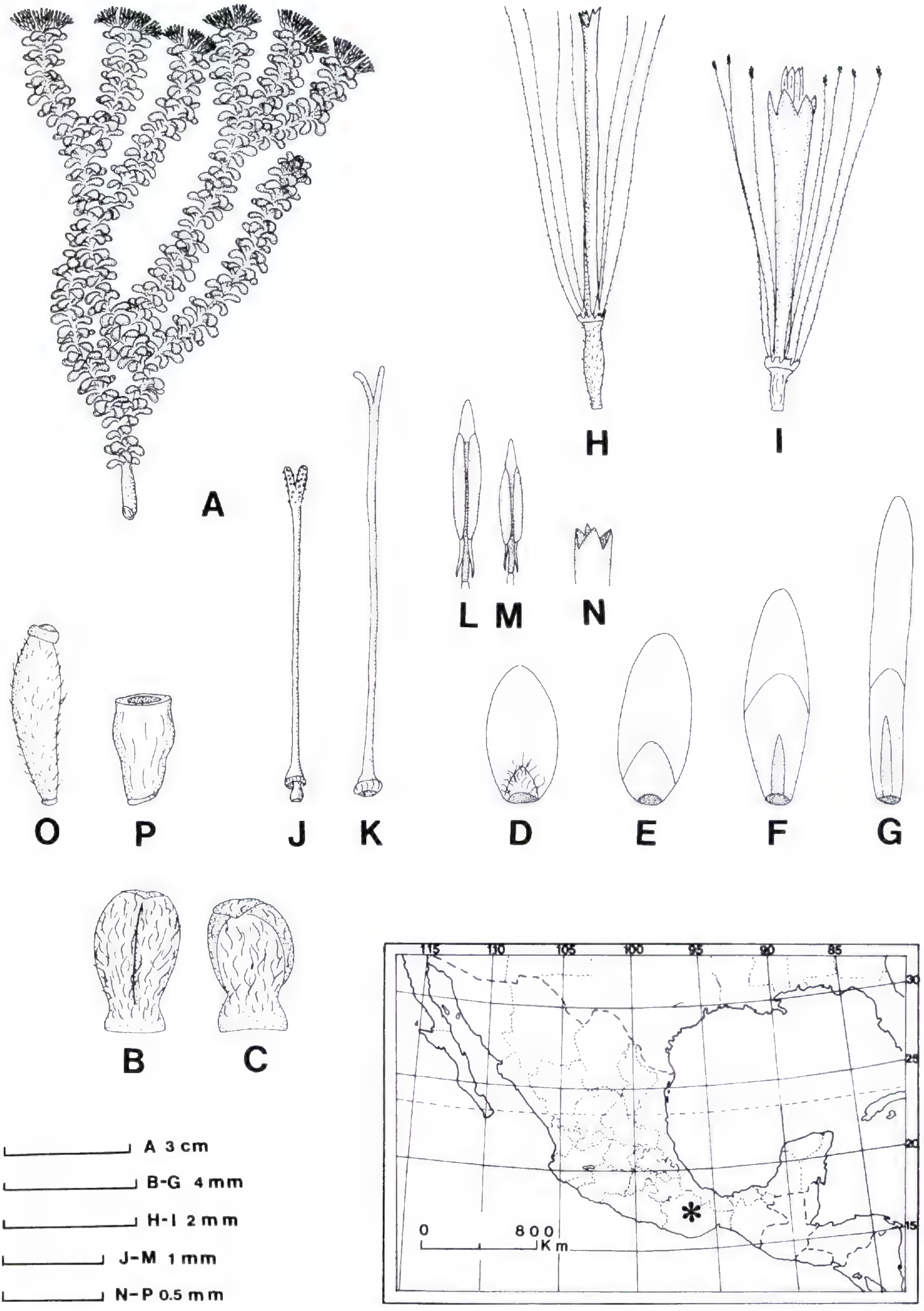
FIGURE 5. *Chionolaena aecidiocephala* (Grierson) Anderberg & Freire.—A. Portion of plant.—B, C. Leaves, leaf adaxial surface (left), leaf abaxial surface (right).—D–G. Involucral bracts.—H. Pistillate floret.—I. Functionally staminate floret.—J. Style of functionally staminate floret.—K. Style of pistillate floret.—L. Stamen of functionally




staminate floret from homogamous capitulum.—M. Stamen of functionally neuter floret from heterogamous capitulum.—N. Top of pistillate floret.—O. Achene of pistillate floret.—P. Ovary of functionally staminate floret from homogamous capitulum. Below: Mexican distribution. A–P, *MacDougall 4129* (S).

suborbicular leaves and purplish bracts. It is closely related to *C. lavandulifolia*: both species have obtuse outer bracts and the capitula arranged in dense umbels.

**2. Chionolaena arbuscula** DC., Prodr. 5: 397. 1836. TYPE: Brazil. Minas Gerais: Marianne, 1833, *M. Vauthier 298* (lectotype, selected here, G; isolectotype, GH, photograph at LP). Figure 6.

Erect, rigid shrubs, with thin woody stems, 50 cm high. *Leaves* narrowly linear, 1–2 cm long, 0.7–1 mm wide with conspicuously revolute margins, glabrous on adaxial side, abaxial surface densely woolly. *Capitula* heterogamous, solitary on the upper branches, sometimes arranged in small, loose, terminal umbels at the ends of the leafy stems. *Involucre* narrowly oblong. Involucral bracts 12–52; outer bracts linear-ovate, acute, 3–3.5 mm long, 1 mm wide, with few long woolly hairs; inner bracts linear elliptic, acute, 3–6 mm long, 0.3–0.5 mm wide. *Florets* 32–65, functionally staminate florets commonly more numerous than the pistillate, occasionally equaling or fewer. *Pistillate florets* 10–32; corollas 1.8–2.4 mm long; achenes oblong, 0.7–1.2 mm long, 0.2–0.5 mm wide, sericeous with long, apically acute, duplex hairs. *Functionally staminate florets* 21–47; corollas 1.8–3.5 mm long; style branches acute, 0.15–0.40 mm long; anthers 1–1.5 mm long with tails shorter than the antheropodium; ovaries sterile, pubescence as in pistillate florets.

*Distribution.* Restricted to the state of Minas Gerais in southeastern Brazil. It occurs in the planalto, which has a temperate climate and a well-marked dry season. *Chionolaena arbuscula* usually grows adjacent to waterfalls on gray, sandy soils at 1,500 m. Flowering collections were made in May, August, January, and February.

*Additional specimens examined.* BRAZIL. MINAS GERAIS: Serra de Itatiaia, *Claussen*, 1839 (GH); Serra do Espinhaço, campo and gallery margin with outcrops, gray sandy soil, ca. 12 km W of Barão de Cocais, base of Serra da Caraça, ca. 1,500 m, periodically flooded crevices adjacent to waterfall, 28 Jan. 1971, *Irwin et al. 29310* (NY); Serra do Espinhaço, riacho margin, cerrado, sedge meadow (brejo) sandstone outcrops and gallery forest, ca. 10 km W of Barão de Cocais gray sandy soil, ca. 1,500 m, 24 Jan. 1971, *Irwin et al. 29023* (NY); Environs de Rio de Janeiro et d'Ouro-Preto-Brésil, 6 Aug. 1885, *Glaziou 14959* (NY); Serra de Ouro Preto, Apr. 1892, *Ule 2602* (HBG); prope Itambe do Matto dentro et in Serra de Piedade, *Martius 843* (M); Serra do Caraça, 1880, *Glaziou 11036* (G), 25 Mar. 1957, *E. Pereira 2637*, *Pabst 3473* (both RB); Serra de Ibitipoca, 15 May 1970, *Krieger & Urbano 8649* (RB); Campos de Ouro Branco, 26 Nov. 1922, *Campos Porto 1218* (RB); Serra do Curral, Belo Horizonte, 20 May 1952, *P. L. Roth 1401* (RB). Sine loco. BRASILIA: *Schuch s.n.* (NY), *Martius 829* (M); in 1903, *L. Damazio 1159* (RB).

*Chionolaena arbuscula* is closely related to *C. lychnophorioides*: both species are erect, rigid, woody shrubs with solitary capitula and achene hairs acute at the apex. *Chionolaena arbuscula* is easily distinguished by its narrowly linear leaves with conspicuous revolute margins and capitula with male florets outnumbering female florets.

**3. Chionolaena capitata** (Baker in Martius) Freire, comb. nov. *Achyrocline capitata* Baker in Martius, Fl. Bras. 6: 117, tab. 39. 1882. *Leucopholis capitata* (Baker) Cufod., Feddes Repert. 31: 329. 1933. SYNTYPES: Brazil. Minas Gerais: Serra de Itatiaia, *Sello 859* (not seen); Rio de Janeiro: *Glaziou 4843* (K, S, US), *Glaziou 5899* (lectotype, selected here, S), *Glaziou 6593* (US), *Glaziou 7723* (G). Figure 7.

*Chionolaena arbuscula* DC. var. *hololeuca* Baker ex Glaz., Mém. Soc. Bot. France 1: 406. 1910. SYNTYPES: Brazil. Rio de Janeiro: Serra de Itatiaia, entre les rochers, *Glaziou 4842* (not seen), *Glaziou 4843* (lectotype, selected here, S; isolectotypes, K, US), *Glaziou 6593* (US), *Glaziou 8768* (G, K).

Weakly woody shrub with multibranched, erect stems, 20–60 cm high. *Leaves* linear, 5–13 mm long, 0.6–1 mm wide with slightly revolute margins, tomentose adaxially, densely lanate abaxially. *Capitula* heterogamous (occasionally homogamous), arranged in dense umbels sessile and terminal on the upper branches. *Involucre* narrowly oblong. Involucral bracts 16–25; outer bracts ovate to linear-ovate, acute, 1.5–3.5 mm long, 0.5–1.5 mm wide; inner bracts linear, acute, 4–8 mm long, 0.4–1 mm wide. *Florets* 5–11, functionally staminate florets slightly more numerous than the pistillate, sometimes equaling, or all functionally

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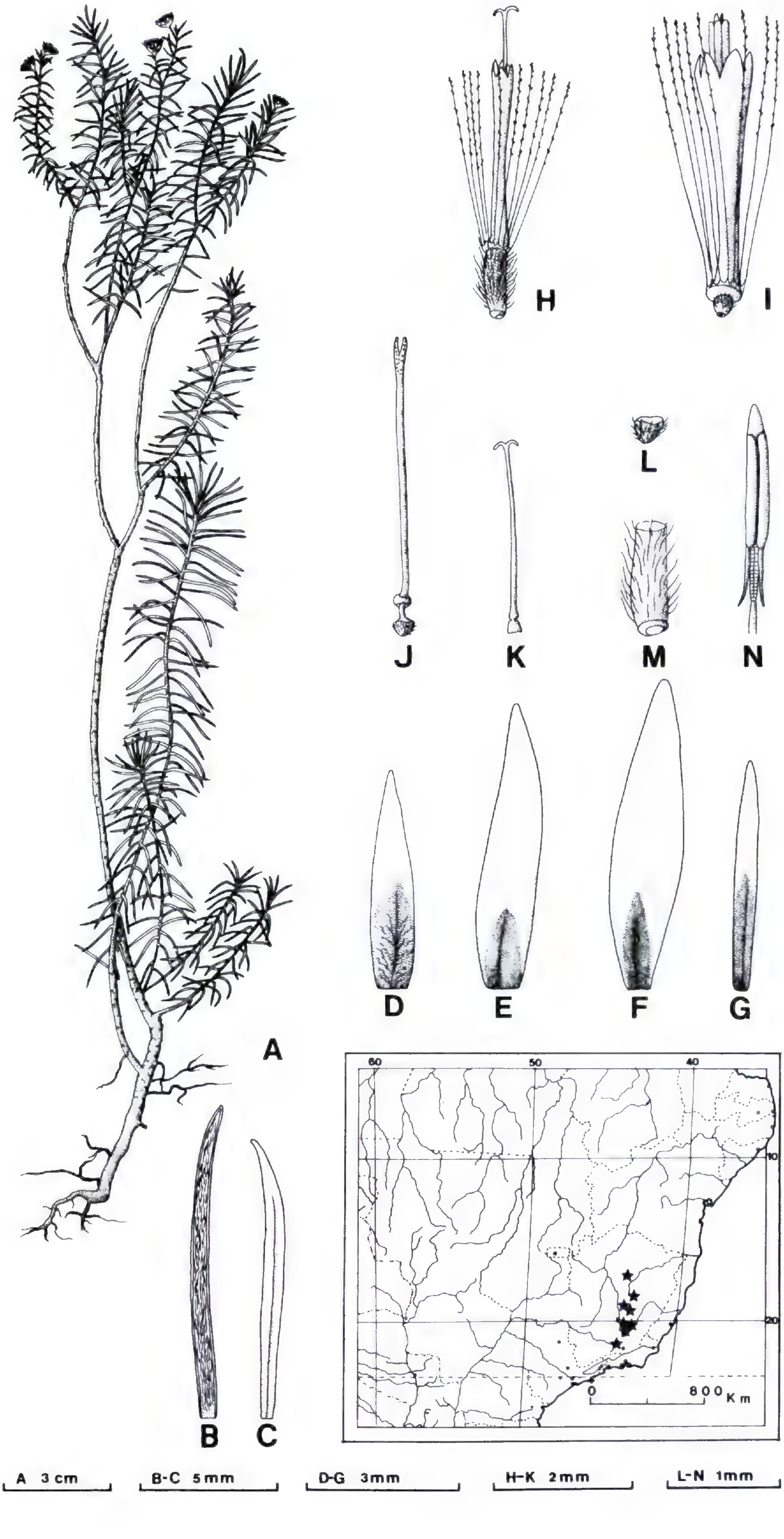
FIGURE 6. *Chionolaena arbuscula* DC.—A. Habit.—B, C. Leaves, abaxial surface (left), adaxial surface (right).—D–G. Involucral bracts.—H. Pistillate floret. I. Functionally staminate floret.—J. Style of functionally staminate floret.—K. Style of pistillate floret.—L. Ovary of functionally staminate floret.—M. Achene of pistillate floret.—N. Stamen. Below: Brazilian distribution. A, *Clausen s.n.* (GH); B–N, *Irwin et al. 29310* (NY).


A
B
C
D
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G
H
I
J
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L
M
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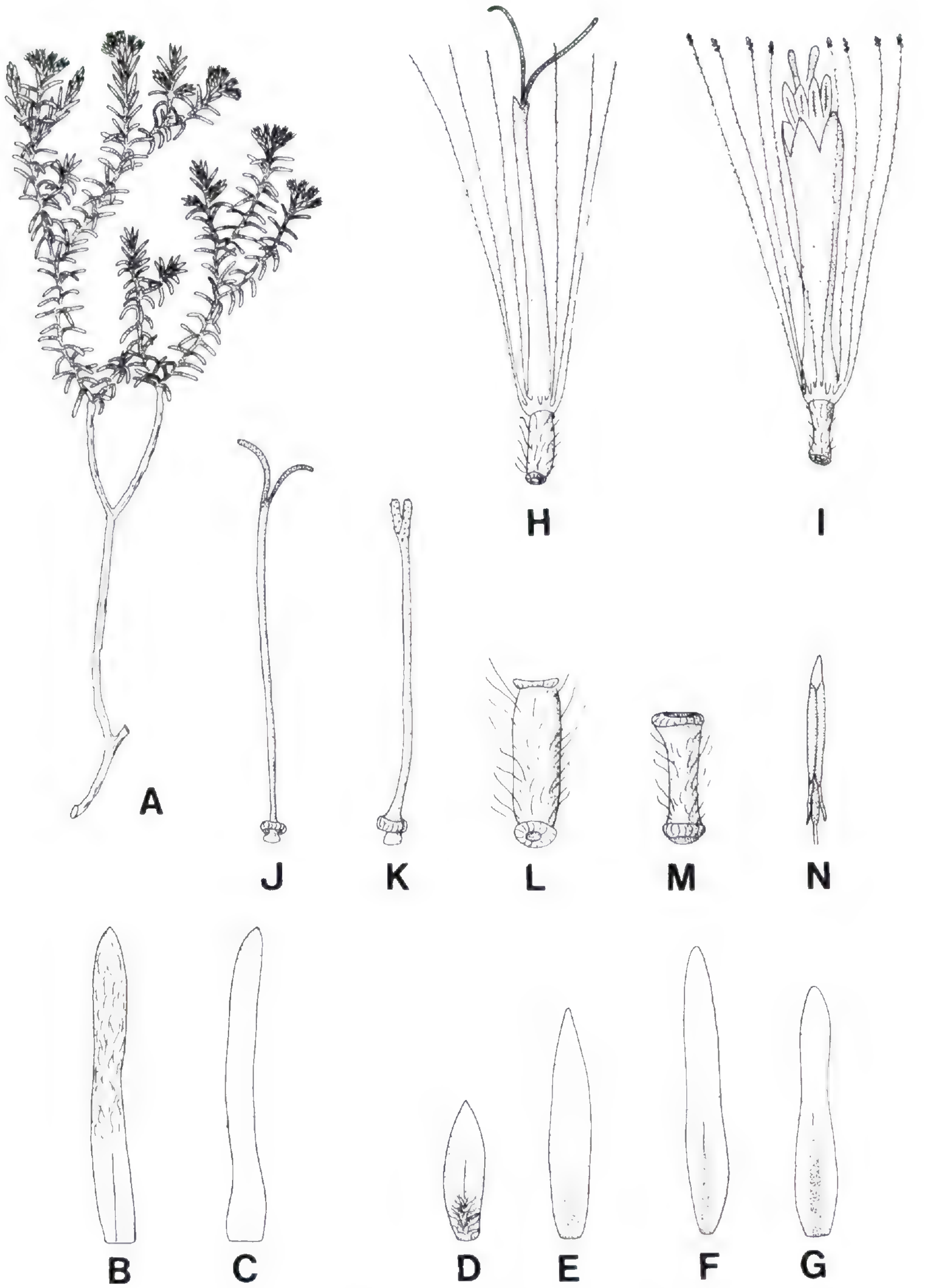
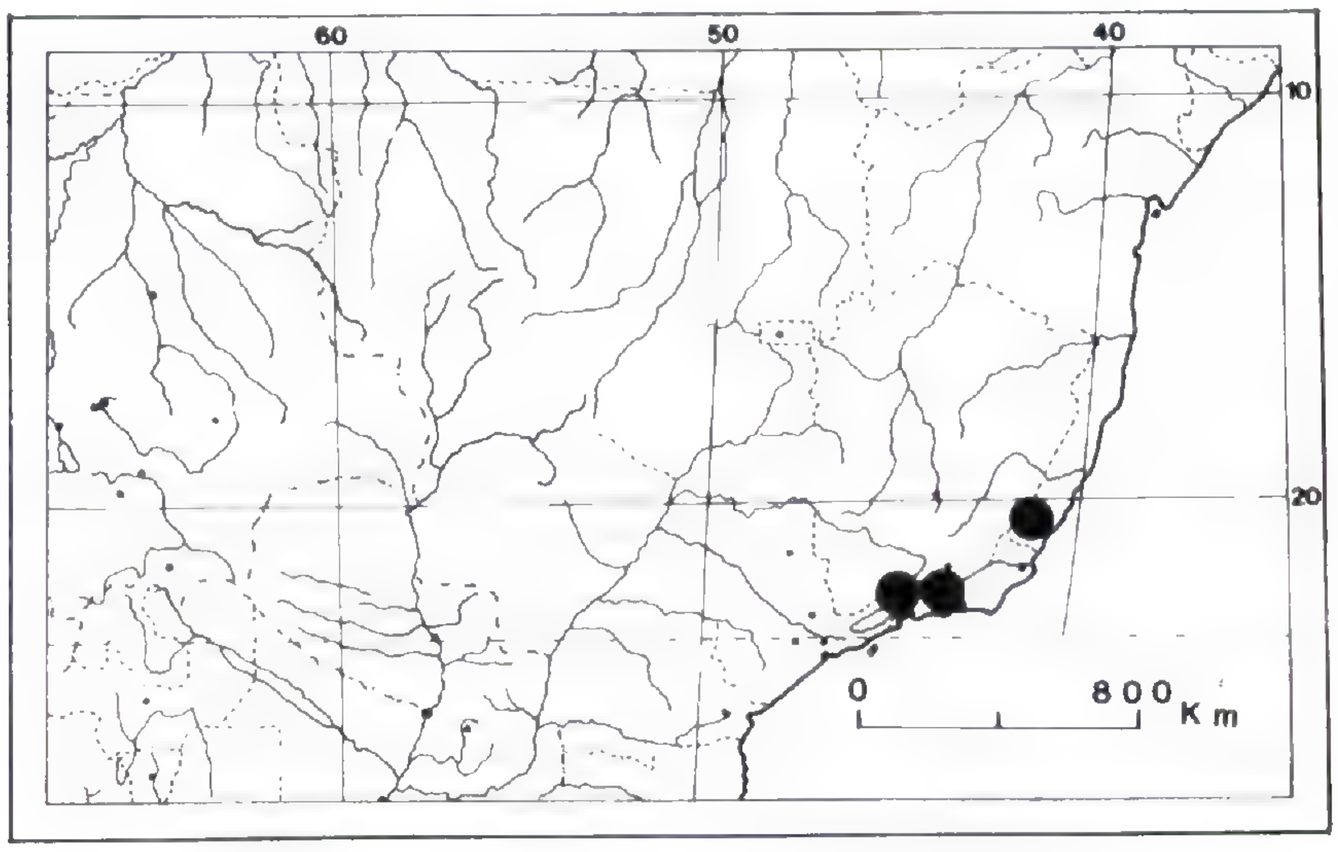
60
50
40
10
20
0
800 Km
A 3 cm
B-C 5 mm
D-G 3 mm
H-K 2 mm
L-N 1 mm




A 3 cm

B-G 2mm

H-N 1mm



staminate. *Pistillate florets* (0–)2–4; corollas 1.5–4 mm long; achenes oblong-elliptic, 0.5–1.2 mm long, 0.25–0.50 mm wide, pubescent with long, apically obtuse, duplex hairs. *Functionally staminate florets* 2–8; corollas 1.8–3.5 mm long; style branches truncate or rounded, rarely subacute, 0–0.4 mm long; anthers 1–1.8 mm long with tails equaling antheropodium; ovaries sterile, contracted toward middle, 0.3–0.8 mm long, 0.15–0.40 mm wide, pubescence as in pistillate florets.

*Distribution.* Restricted to the states of Minas Gerais, Rio de Janeiro, and Paraná of southeastern Brazil. *Chionolaena capitata* is found in the planalto, which has a temperate climate and a slightly to well-marked dry season. It often grows in rocky places, between 2,300 and 2,850 m. Flowering collections were made from April to October.

*Additional specimens examined.* BRAZIL. MINAS GERAIS: Serra do Caparaó, Pico de Calçado, 2,850 m, 25 Sep. 1941, *A. C. Brade 17013* (NY); Pico Luis Ignasio, 2,300 m, 9 Sep. 1941, *A. C. Brade 16898* (NY); slope of Pontão Crystal?, in rocks, 30 Apr.–4 May 1925, *Chase 9708* (GH); Subida Agulhas Negras, ca. 2,400 m, 16 Aug. 1969, *Sucre 5765* (COL). PARANA: *Dusén s.n.* (S). RIO DE JANEIRO: Itatiaia, 2,300 m, Aug. 1933, *Brade 12659* (NY); 2,300–2,400 m, 23 Aug. 1960, *O. Handro 9423* (NY); 2,350 m, terreno pedregoso, 29 Apr. 1977, *Joly C. A. et al. 6790* (NY); 2,400 m, 4/10 June 1913, *F. Tamandaré 6384* (S); Agulhas Negras, 3,000 m, 4/10 June 1913, *F. Tamandaré & A. C. Brade 6383* (S), 19/27 July 1901, *Hemmendorff 633* (S); Municipio Rezende, Parque Nacional de Itatiaia, planalto, proximo do abrigo Rebonças, campos de altitude 2,400 m, 9 Oct. 1981, *Martinelli 7762* (RB); Pedra do Altar, 2,400 m, 1937, *A. C. Brade 15599* (NY); "Felsritzen des Kegels," (Wawra 396 (NY); planalto, km 16 de la carretera, ca. 2,300 m, 25/26 May 1961, *Cabrera & Fabris 14212* (GH, LP); Serra da Pedra assentado, Retiro, 5 June 1902, *Dusén 468* (S); Rio Bonito, Bracaña, 4 July 1978, *Lua & Nogueira 30* (RB); Serra do Itatiaia, 26 Dec. 1895, *Ule 3913* (HBG).

*Chionolaena capitata* is recognized by its adaxially and abaxially pubescent, linear leaves and dense umbellate clusters of capitula.

Glaziou (1910) mentioned the variety *hololeuca* ex Baker and cited the following specimens *4842*, *4843*, *6593*, and *8768*. Analysis of these specimens, except *4842*, shows that they belong to *C. capitata* because they have small leaves and few-flowered capitula arranged in dense umbels. Furthermore, the specimens *Glaziou 4843* and *6593* form part of the type material cited by Baker (1882) for *Achyrocline capitata* (= *Chionolaena capitata*).

4. **Chionolaena columbiana** S. F. Blake, J. Wash. Acad. Sci. 25: 312. 1935. TYPE: Colombia. Paramos of the Sierra Nevada de Santa Marta, about 30 mi. inland from Dibulla, ca. 4,390 m, July 1932, *William Seifriz 494* (holotype, US). Figure 8.

Caespitose shrub with weakly woody stems, 15–30 cm high. *Leaves* linear-obovate 1.3–4.5 cm long, 3–4.5 mm wide with slightly revolute margins, tomentose adaxially, densely lanate abaxially. *Capitula* heterogamous, arranged in dense umbels surrounded by leaves of the same shape as the stem leaves, umbels supported at maturity by a woolly, thin peduncle with a few scattered, generally rather small leaves. *Involucre* obdeltate. Involucral bracts 25–27; outer bracts ovate, acuminate, 4 mm long, 1.5 mm wide; inner bracts linear elliptic, obtuse, 3–5 mm long, 0.5–1 mm wide. *Florets* 13–20, pistillate florets slightly more numerous than the functionally staminate. *Pistillate florets* 7–9; corollas 1–2.8 mm long; achenes oblong, 0.3–0.8 mm long, 0.15–0.20 mm wide, glabrous. *Functionally staminate florets* 6–8; corollas 1.5–3 mm long; style branches rounded, 0.3–0.4 mm long; anthers 1 mm long with tails equaling antheropodium; ovaries sterile, flattened, 0.3–0.7 mm long, 0.15–0.20 mm wide, glabrous.

*Distribution.* Restricted to northern Colombia on the Sierra de Santa Marta and the Sierra de Perijá. It grows in rocky places, between 3,000 and 3,900 m. Flowering collections were made from April to November.

*Additional specimens examined.* COLOMBIA. MAGDALENA: Cordillera Oriental, Sierra de Perijá, 12 km ENE of Manaure, 48 km E of Valledupar, 1 km from the Venezuelan border, 3,000 m, 5 Feb. 1945, *M. L. Grant 10864* (NY, US); Sierra de Perijá, plain between Cerro Venado and Cerro Avión, paramo 3,270–3,350 m, 8 Nov. 1959, *Cuatrecasas & Castañeda 25115* (US); Sierra Perijá, Tres Tetas (south peak, 3,000 m, 28 Apr.–4 May 1942, *Carriker 15* (US); Mun. La Paz, frontera colombo–venezolana, Serranía de Perijá, entre los cerros El Venado y El Avión, 3,200–3,600 m, 3 Mar. 1959, *Romero & Castañeda 7356* (MO); Sierra Nevada de Santa Marta, 1 km S of laguna Río Frío, 3,800 3,900,

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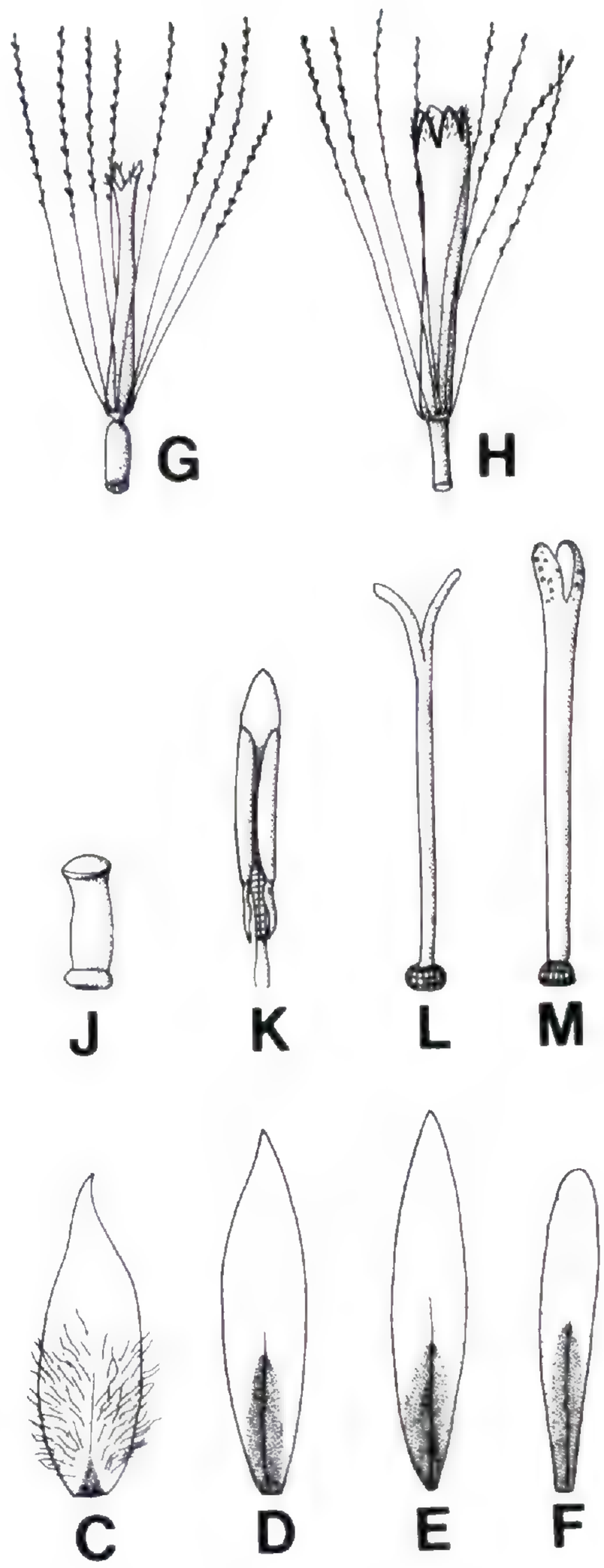
FIGURE 7. *Chionolaena capitata* (Baker in Martius) Freire. — A. Portion of plant. — B, C. Leaves, abaxial surface (left), adaxial surface (right). — D–G. Involucral bracts. — H. Pistillate floret. — I. Functionally staminate floret. — J. Style of pistillate floret. — K. Style of functionally staminate floret. — L. Achene of pistillate floret. — M. Ovary of functionally staminate floret. — N. Stamen. Below: Brazilian distribution. A–N, *Hemmendorff 633* (S).



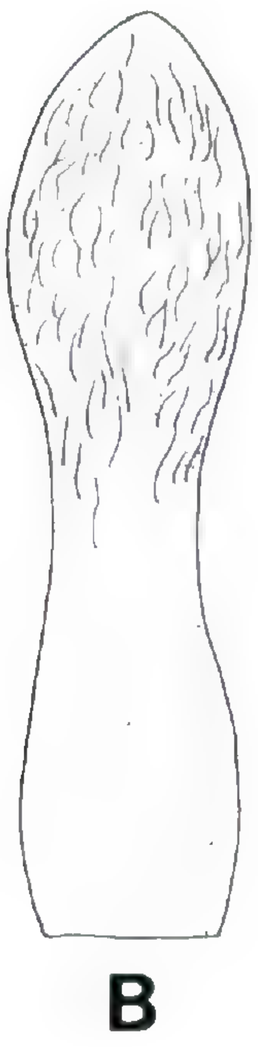

A 3 cm

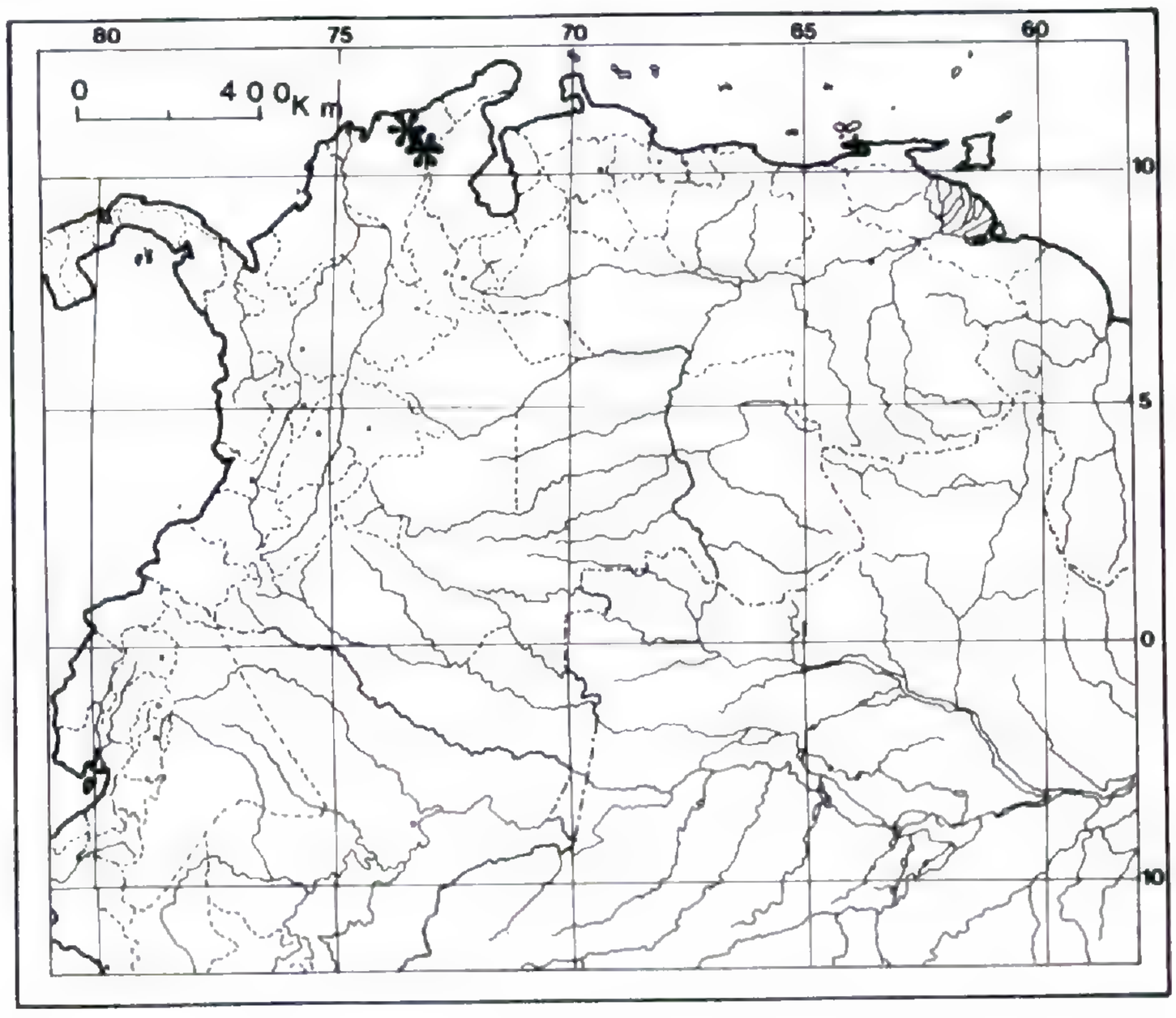
B 1 cm

C–F 5 mm

G–H 2 mm

I–M 1 mm



ca. 10°55′N, 73°53′W, 30 July 1972, *J. H. Kirkbride Jr. & E. Forero 1803* (MO, NY, RB, US); Sierra Nevada de Santa Marta, Transecto del Buritaca (Filo La Cumbre), 3,850 m, 19 Aug. 1977, *Rangel et al. 988* (U); Sierra Nevada de Santa Marta, alrededores de cabeceras de Río Ancho, Paramo de Macotama, on rock outcrop of high ridge SE of campsite at joining of two streams, 3,840 m, 13 Feb. 1959, *Barclay & Juajibioy 6927* (US).

*Chionolaena columbiana* is closely related to *C. isabellae* from southern Brazil: both species have obovate leaves and pedunculate capitulescences, but the former differs by its densely umbellate clusters of capitula and acuminate outer bracts.

**5. Chionolaena concinna** (A. Gray) Anderberg & Freire, Notes Roy. Bot. Gard. Edinburgh 46(1): 37–41. 1989. *Gnaphalium concinnum* A. Gray, Proc. Amer. Acad. Arts 15: 34. 1879. *Anaphalis concinna* (A. Gray) Grierson, Notes Roy. Bot. Gard. Edinburgh 31: 392. 1972. TYPE: Mexico. San Luis Potosí: 22°N, alt. 6,000–8,000 ft., in 1878, *Parry & Palmer 423* (lectotype, designated by Anderberg & Freire (1989), GH; isolectotypes, BM, E). Figure 9.

Subshrub, with thin, subdichotomously branched stems, 20–40 cm high. *Leaves* obovate, subpetiolate, obtuse, 1.5–2.5 cm long, 4–7 mm wide with slightly revolute margins, tomentose adaxially, densely whitish lanate abaxially. *Capitula* heterogamous, arranged in sessile and terminal corymbs that later become deeply lateral. *Involucre* obdeltate. Involucral bracts 30–34; outer bracts ovate, acute, 4 mm long, 1.5 mm wide; inner bracts stipitate, obtuse, 6 mm long, 0.5 mm wide. *Florets* 36–42, pistillate florets slightly more numerous than, ± equaling, or slightly fewer than the functionally staminate. *Pistillate florets* ca. 20; corollas 2.5–2.9 mm long; achenes elliptic, 0.6–0.8 mm long, 0.3 mm wide, pubescent with short, apically obtuse, duplex hairs. *Functionally staminate florets* 16–22; corollas 1.5–3 mm long; style branches truncate, 0.4 mm long; anthers 1.5 mm long with tails equaling antheropodium; ovaries sterile, strongly contracted, 0.2–0.6 mm long, 0.10–0.15 mm wide, pubescence as in pistillate florets.

*Distribution.* Restricted to central Mexico. Known only from the original site, which is at 22°N between 1,800 and 2,400 m. Flowering collections were made in September.

*Additional specimen examined.* MEXICO. SAN LUIS POTOSI: Sep. 1879, *Schaffner 222* (BM, GH).

*Chionolaena concinna* is distinguished from other Mexican species of the genus by its slender, subdichotomously branched stems and obovate leaves.

**6. Chionolaena chrysocoma** (Wedd.) Freire, comb. nov. *Oligandra chrysocoma* Wedd., Chlor. Andina I: 158. 1855. *Pseudoligandra chrysocoma* (Wedd.) Dillon & Sagást., Taxon 39: 125. 1990. TYPE: Colombia. Nouvelle Grenade, prov. de Río Hacha, Sierra Nevada, 3,800 -4,300 m, 1852, *Schlim 809* (holotype, P). Figure 10.

Erect, rigid, multibranched shrub, 30–40 cm high. *Leaves* closely appressed to stem, linear, acute, 4–6 mm long, 0.8–1 mm wide, glabrous adaxially, densely whitish lanate and completely concealed by the revolute margins abaxially. *Capitula* heterogamous, arranged in dense umbels sessile and terminal on the upper branches. *Involucre* narrowly oblong. Involucral bracts 21–31; outer bracts linear-ovate, acute, 4–4.5 mm long, 0.5–0.8 mm wide; inner bracts linear elliptic, slightly acuminate, 5–6 mm long, 0.6–0.2 mm wide. *Florets* 9–13, pistillate florets slightly more numerous than the functionally staminate. *Pistillate florets* 4–8; corollas 2.2–3.2 mm long; achenes oblong, 0.6–0.8 mm long, 0.25–0.30 mm wide, glabrous. *Functionally staminate florets* 3–6; corollas 2–4 mm long; style branches rounded to obtuse, 0.2–0.4 mm long; anthers 1.5 mm long with tails equaling antheropodium; ovaries sterile, flattened, 0.4–0.7 mm long, 0.2 mm wide.

*Distribution.* Restricted to northern Colombia on the Sierra de Santa Marta. This species grows at the highest elevations of any species in the genus (between 3,300 and 4,300 m). Flowering collections were made in March and August.

*Additional specimen examined.* COLOMBIA. MAGDALENA: Sierra Nevada de Santa Marta, Transecto del Buritaca, Filo La Cumbre, 3,300 m, Aug. 1977, *O. Rangel & A. Cleef 934* (US).

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FIGURE 8. *Chionolaena columbiana* S. F. Blake.—A. Portion of plant.—B. Leaf adaxial surface.—C–F. Involucral bracts.—G. Pistillate floret.—H. Functionally staminate floret.—I. Achene of pistillate floret.—J. Ovary of functionally staminate floret.—K. Stamen.—L. Style of pistillate floret.—M. Style of functionally staminate floret. Below: Colombian distribution. A—M, *Kirkbride & Forero 1803* (MO).

*Chionolaena chrysocoma* is distinguished from other species of the genus by its appressed leaves. It is similar to *C. phylicoides*: both species exhibit narrowly oblong involucres, capitula arranged in dense umbels, and lower leaf surfaces completely concealed by the revolute margins.

7. **Chionolaena eleagnoides** Klatt, Leopoldina 23: 88. 1887. *Gnaphalium eleagnoides* (Klatt) S. F. Blake, Contr. U.S. Natl. Herb. 23: 1511. 1926. [*Gnaphalium hypochaionaeum* Sch. Bip. ex Klatt, Leopoldina 23: 88. 1887, sub *C. eleagnoides*, as synonym, nomen nudum.] TYPE: Mexico. Pelado, Aug. 1841, *Liebman 316* (holotype, C; isotypes (fragment), GH; photograph ex C in US). Figure 11.

Moderately branched shrub with weak, woody stems. *Leaves* broadly obovate, narrowed at the base, 3–4.5 cm long, 11–12 mm wide with slightly revolute margins, adaxially arachnoid pubescent, densely whitish lanate abaxially. *Capitula* heterogamous, arranged in corymbs sessile and terminal to the stems. *Involucre* obdeltate. Involucral bracts ca. 42; outer bracts ovate, obtuse, 2.5 mm long, 1.5 mm wide; inner bracts oblong obovate, 3 mm long, 1 mm wide. *Florets* 30–34, functionally staminate florets slightly more numerous than pistillate or equaling them. *Pistillate florets* 15–16; corollas 1.5–2.5 mm long; achenes oblong, 0.5 mm long, 0.25 mm wide, glabrous. *Functionally staminate florets* 15–18; corollas 1.2–2.5 mm long; style branches rounded, 0.2 mm long; anthers 1.8–2 mm long with tails equaling antheropodium; ovaries sterile, flattened, 0.3 mm long, 0.2 mm wide, glabrous.

*Distribution.* Known only from the type locality at Pelado, Mexico, at 3,600 m. Flowering collections were made in August.

*Chionolaena eleagnoides* is recognized by its broad, obovate leaves with slightly revolute margins.

8. **Chionolaena isabellae** Baker in Martius, Fl. Bras. 6: 130, tab. 46. 1882. SYNTYPES: Brazil. Rio de Janeiro: Serra de Itatiaia, 22 Jan. 1873, *Glaziou 6601* (lectotype, selected here, S; isolectotypes, G, UC); Serra de Itatiaia, 10 Jan. 1876, *Glaziou 4840* (NY, S). Figure 12.

*Chionolaena glaziovii* Baker in Martius, Fl. Bras. 6: 130. 1882. TYPE: Brazil. Minas Gerais: sommet de la Sierra de Tirapitinoja, 2,120 m, 20 Nov. 1876, *Glaziou 8769* (lectotype, selected here, P; isolectotypes, G, S).

*Chionolaena innovans* Wawra, Itin. Princ. S. Coburgi 2: 30. 1888. TYPE: Brazil. Itatiaia, Gipfel des Kegels, 1879, *Wawra 420* (holotype, W).

Erect, rigid, multibranched shrub, 15–40 cm high. *Leaves* narrowly obovate, 1.3–2.2 cm long, 3–5 mm wide with slightly revolute margins, tomentose adaxially, densely lanate and whitish abaxially. *Capitula* homogamous, arranged in dense umbels, these umbels aggregated in spreading corymbs terminal to the stems supported at maturity by a peduncle, 1.5–2.5 cm long, wholly devoid of leaves. *Involucre* obdeltate. Involucral bracts 18–28, yellow; outer bracts broadly ovate, obtuse, 2.5–3 mm long, 1.5–2 mm wide; inner bracts linear oblong, obtuse, 4–5 mm long, 0.4–1 mm wide. *Florets* 12–31, all perfect (apparently with embryo developed); corollas 2–3.2 mm long; style branches rounded, 0.3–0.5 mm long; anthers 1–1.3 mm long with tails equaling or slightly exceeding antheropodium; achenes oblong, 0.5–0.9 mm long, 0.2–0.4 mm wide, pubescent with long, apically acute, duplex hairs.

*Distribution.* Restricted to the states of Minas Gerais and Rio de Janeiro of southeastern Brazil. This species occurs between 2,000 and 3,000 m.

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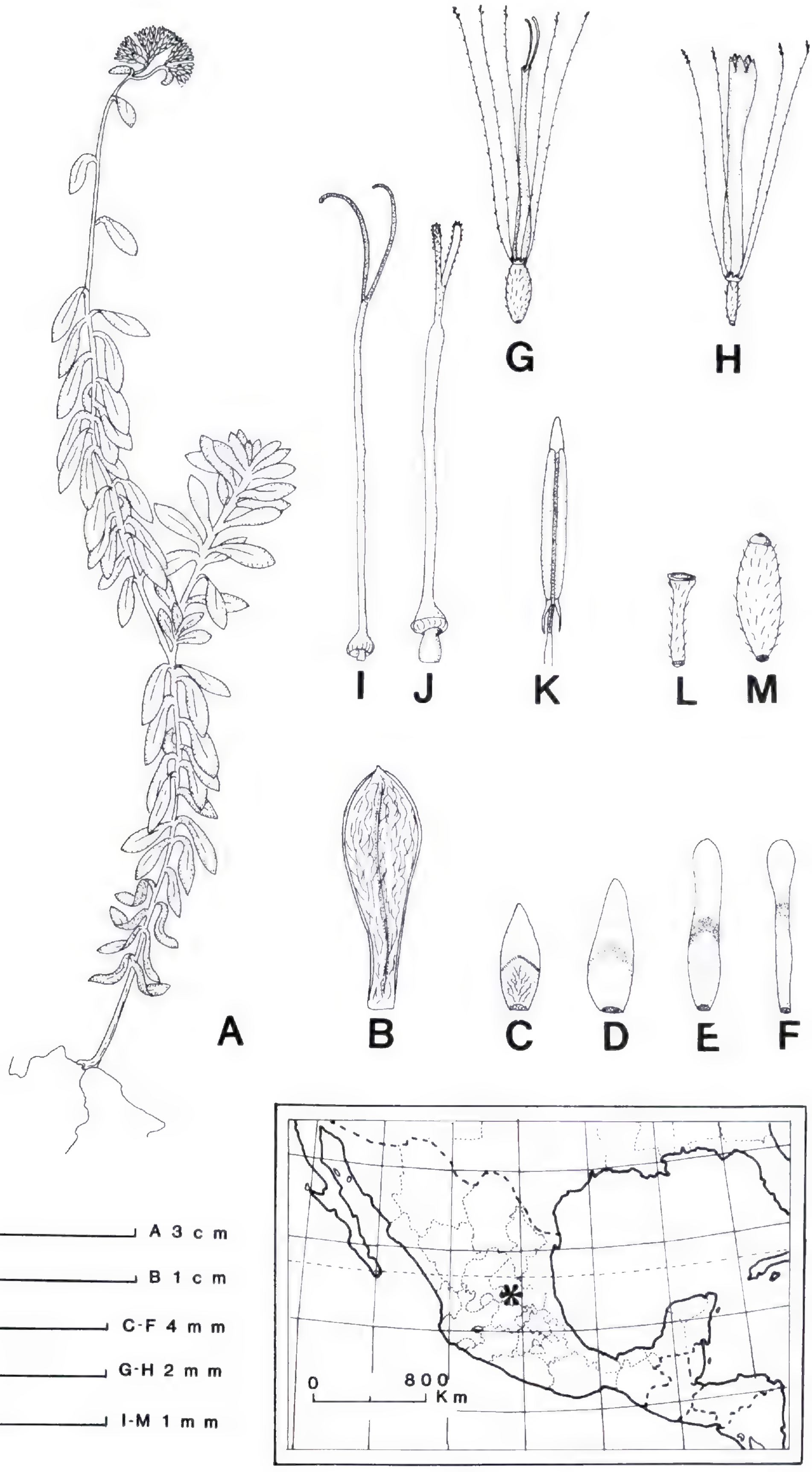
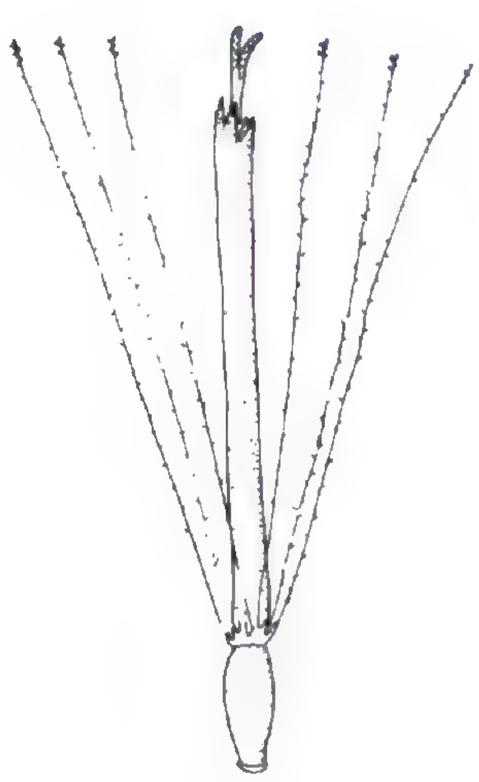
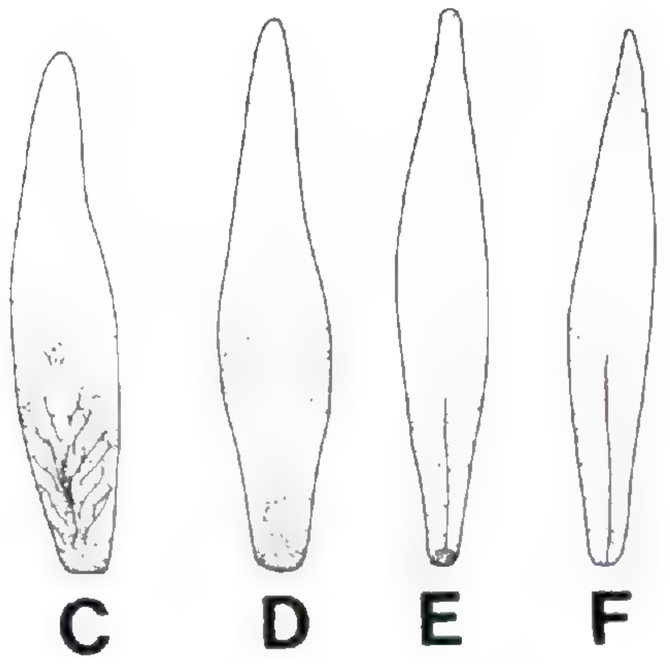
FIGURE 9. *Chionolaena concinna* (A. Gray) Anderberg & Freire. A. Habit.—B. Leaf abaxial surface.—C–F. Involucral bracts. G. Pistillate floret. H. Functionally staminate floret.—I. Style of pistillate floret.—J. Style of functionally staminate floret.—K. Stamen.—L. Ovary of functionally staminate floret.—M. Achene of pistillate floret. Below: Mexican distribution. A, *Parry & Palmer 423* (E); B M, *Parry & Palmer 423* (BM).

FIGURE 10. *Chionolaena chrysocoma* (Wedd.) Freire. A. Portion of plant.—B. Leaf abaxial surface. C F. Involucral bracts.—G. Pistillate floret.—H. Functionally staminate floret.—I. Stamen.—J. Style of pistillate floret. K. Style of functionally staminate floret.—L. Top of pistillate floret.—M. Achene of pistillate floret.—N. Ovary of functionally staminate floret. Below: Colombian distribution. A–N, *Schlim 809* (P).

FIGURE 11. *Chionolaena eleagnoides* Klatt. A. Portion of plant. B. Leaf abaxial surface.—C–F. Involucral bracts. G. Pistillate floret.—H. Functionally staminate floret.—I. Stamen. J. Style of pistillate floret.—K. Style of functionally staminate floret. L. Ovary of functionally staminate floret. M. Achene of pistillate floret. Below: Mexican distribution. A–M, *Liebman 316* (C).


A
B
C
D
E
F
G
H
I
J
K
L
M
A 3 cm
B 1 cm
C-F 4 mm
G-H 2 mm
I-M 1 mm
0
800
Km



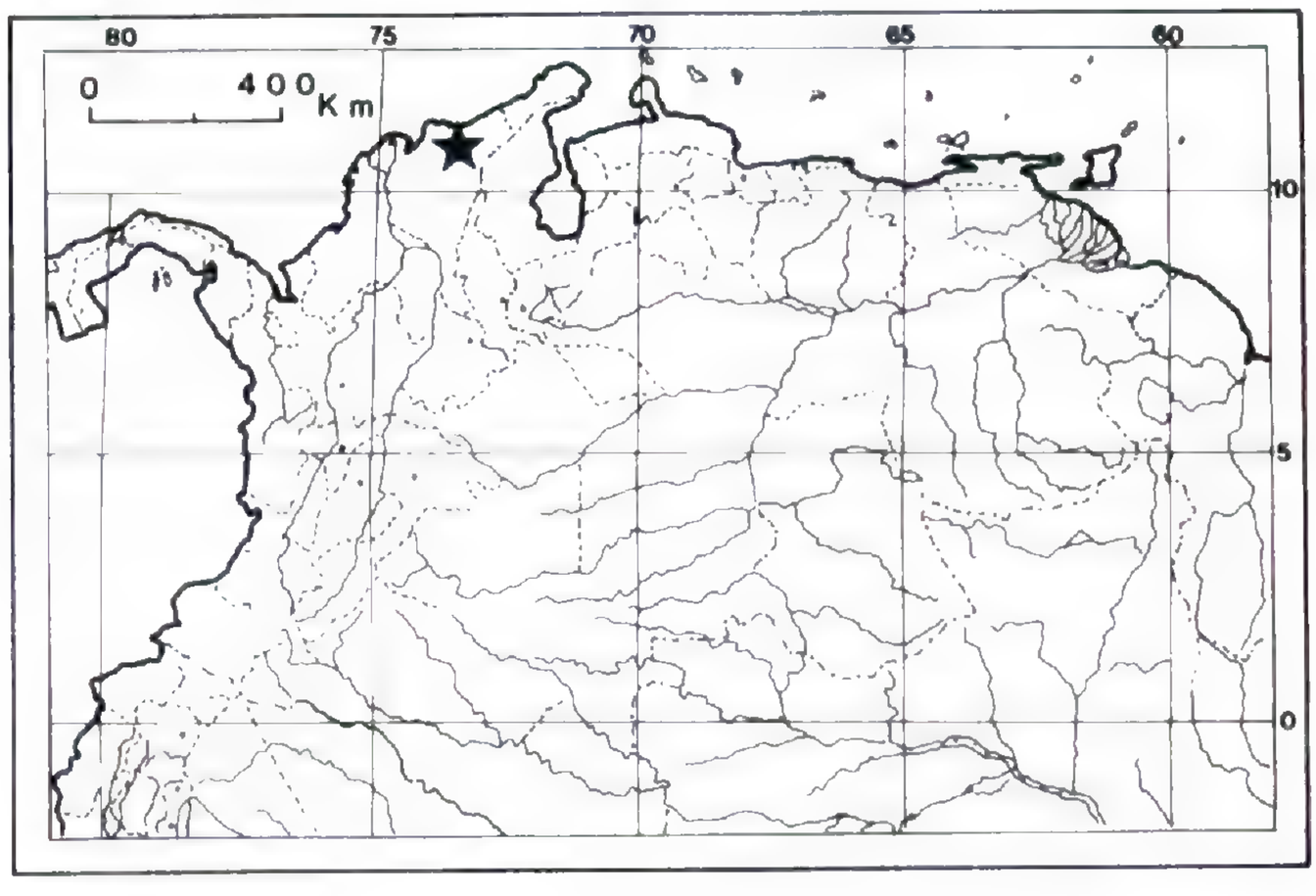



A 3 cm

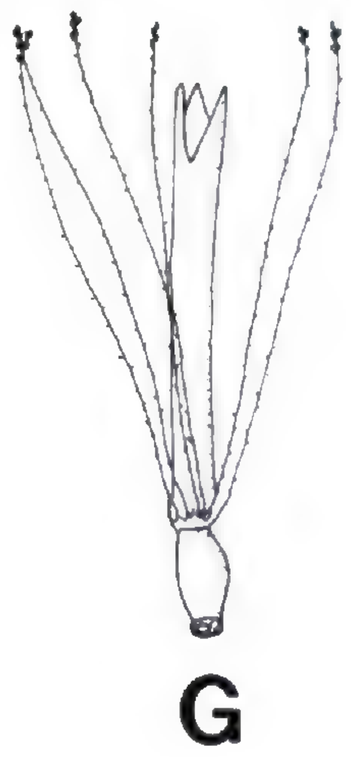
C-F 2 mm

B,G-K 1 mm

L-N 0.5 mm



A



G

H

I

J

K

B

L

M

C

D

E

F

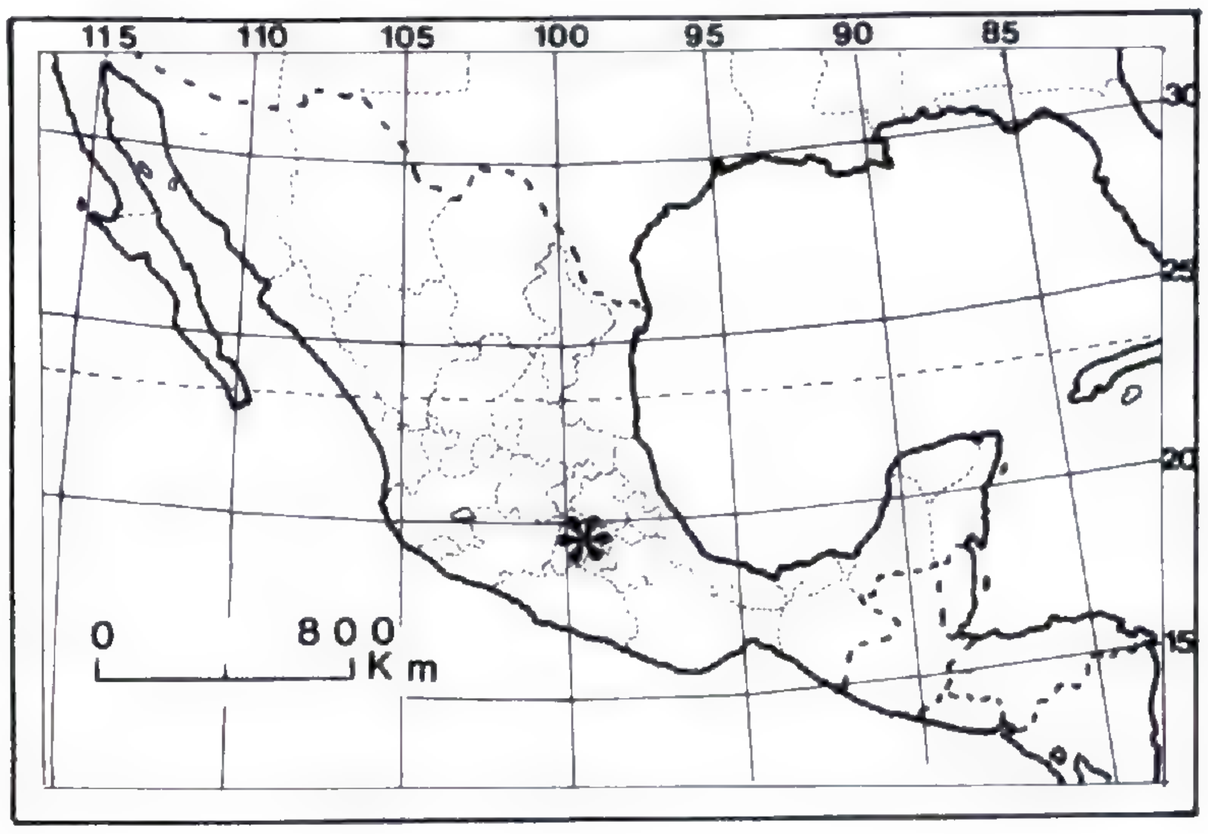
A 3 cm

B 1 cm

C-F 2 mm

G-I 1 mm

J-M 0.5 mm



A 3 cm

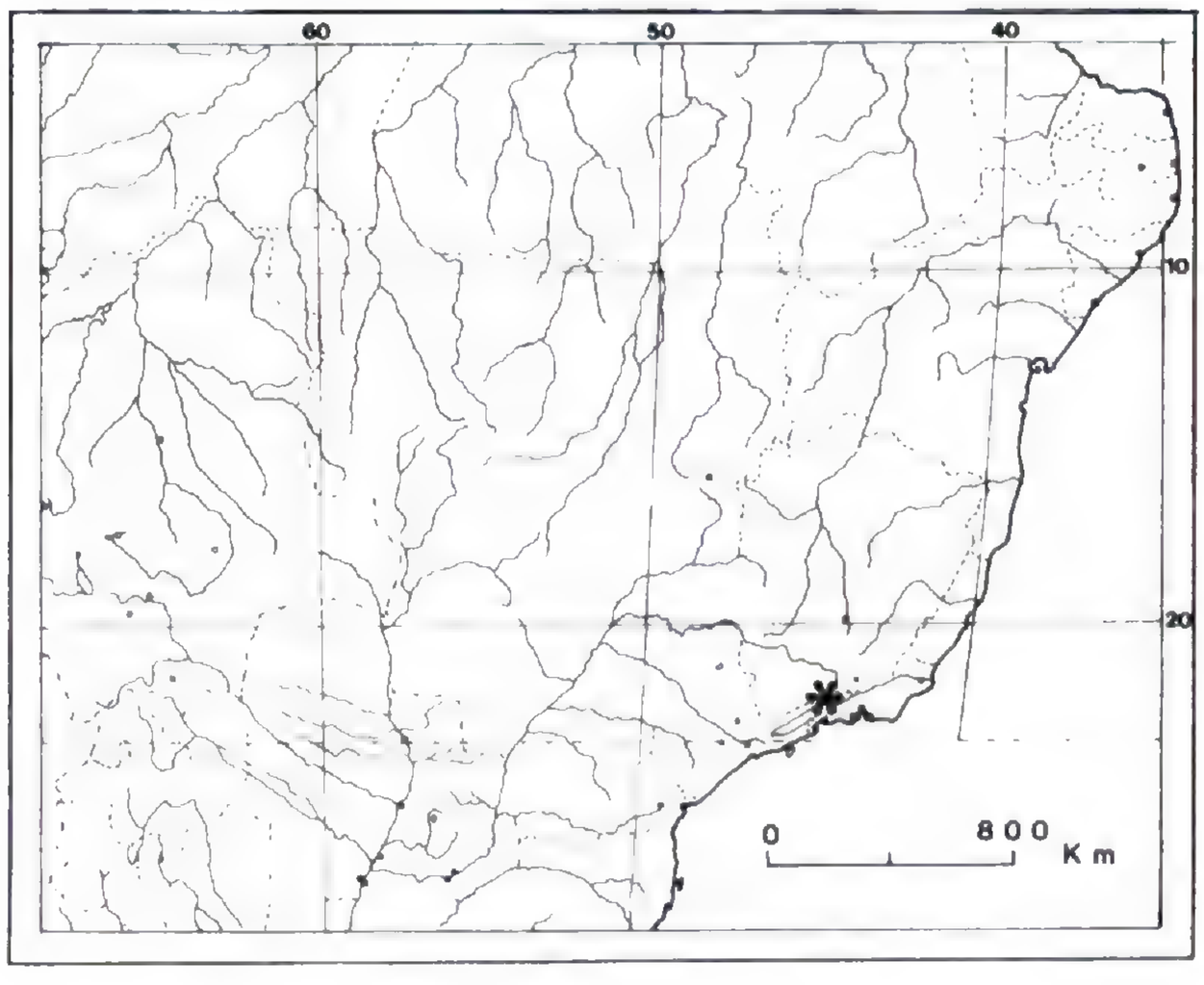
B 6 mm

C-F 3 mm

G 2 mm

H,K 1 mm

I,J 1 mm



Flowering collections were made from February to December, except in July and August.

*Additional specimens examined.* BRAZIL. MINAS GERAIS–RIO DE JANEIRO: Municipio de Itamonte, Parque Nacional do Itatiaia, estrada para Agulhas, 2,000 2,450 m, 2 May 1985, *G. Martinelli, F. Zuloaga & M. Vazguez Avila 10843* (NY); Parque Nac. do Itatiaia, km 17, 12 Mar. 1947, *Guchioni 940* (LP); Itatiaia, Pedra do Altar, 2,400 m, Mar. 1937, *A. C. Brade 15596* (NY); almost on the summit of the Mt. Itatiaia, 3,000 m, 26 Dec. 1915, *Oakes Ames s.n.* (GH); Itatiaia, 2,450 m, 18 Dec. 1968, *Merxmüller & Sammuel 25605* (M); Serra do Itatiaia, Agulhas Negras, 3,000 m, 4–10 June 1913, *Brade 6385* (S), 27 July 1901, *Hemmendorff 632* (S), 9 June 1902, *Dusén 542* (S); Itatiaia, 2,400 m, 9 Sep. 1933, *Brade 12733, 21260* (both RB); 2,500 m, May 1950, *Brade 20282* (RB); Serra do Itatiaia, colhina no pico das Agulhas Negras, 3,000 m, May 1913, *Brade 757* (RB); Itatiaia, Prateleiras, 2,200 m, 8 Feb. 1945, *Brade 17421* (RB), 12 Apr. 1975, *Camerik 29* (U); Campo Itatiaia, 13 May 1906, *Luederwaldt 16733 pro parte* (US), 3 Dec. 1964, *Vianna 197* (RB); Parque Nac. do Itatiaia, vicinity of Abrigo Rebouças "gregarious," 2,350 m, 1 Feb. 1967, *Lindeman & Haas 4134* (U); road from sede do Parque Nacional do Itatiaia to planalto, small valley near broadcasting station, 2,200 m, 16 Apr. 1967, *Lindeman & Haas 5197* (U); Sitio de Ramos, Itatiaia, 2,300 m, Feb. 1899, *Gounelle s.n.* (G); Felson, region Lagoa, 2,300 m, Serra do Itatiaia, 27 Feb. 1895, *Ule 3374* (HBG).

*Chionolaena isabellae* is closely related to *C. columbiana*: both species have obovate leaves and a capitulescence supported by a slender peduncle. *Chionolaena isabellae* is distinguished from *C. columbiana* by its corymbosely arranged, homogamous capitula and its villous achenes with apically acute, duplex hairs.

**9. Chionolaena jeffreyi** H. Robinson, Phytologia 55: 121. 1984. TYPE: Brazil. Municipio de Rio Contas, Pico das Almas a 18 km NW de Rio de Contas, 1,600–1,850 m, 24 July 1979, *R. M. King et al. 8141* (holotype, RB not seen; isotypes, CEPEC not seen, MO not seen, US). Figure 13.

Subshrub, weakly woody, multibranched, with slender ascendent stems, 10–20 cm high. *Leaves* linear-elliptic, narrowed at the base, 3 8 mm long, 1–2 mm wide with slightly revolute margins, tomentose adaxially, densely lanate abaxially. *Capitula* heterogamous, solitary on the upper branches. *Involucre* obdeltate. Involucral bracts 20–25; outer bracts 3.5 mm long, 1.2 mm wide; inner bracts 4.5 mm long, 1 mm wide. *Florets* 23–26, pistillate florets slightly fewer than the functionally staminate. *Pistillate florets* 8–11; corollas 2–2.5 mm long; achenes oblong elliptic, 0.7–0.8 mm long, 0.3 mm wide, pubescent with long, apically obtuse, duplex hairs. *Functionally staminate florets* 15–25; corollas 2–2.8 mm long; style branches rounded, 0.2 mm long; anthers 0.7–1 mm long with tails equaling or slightly exceeding anthheropodium; ovaries sterile, 0.15 mm long, 0.20 mm wide, pubescence as in pistillate florets.

*Distribution.* *Chionolaena jeffreyi* is the only species endemic to the state of Bahia in Brazil, where the climate is temperate with long dry periods. This species is found growing in damp, shady places, between 1,600 and 1,850 m. Flowering collections were made in March and July.

*Additional specimen examined.* BRAZIL. BAHIA: middle and upper NE slopes of the Pico das Almas ca. 25 km WNW of the Vila do Rio de Contas, sandstone conglomerate metamorphic and quartzite rock outcrop with associated scrubby vegetation with damp flushes and grassland and marsh in some areas, ca. 41°57′W, 13°33′S, 1,600–1,850 m, 19 Mar. 1977, *R. M. Harley et al. 19677* (paratypes, NY, RB—2 sheets, U, US).

*Chionolaena jeffreyi* is distinguished from other species of the genus because of its short petiolate, elliptic leaves, solitary capitula, and weakly woody, ascendent stems.

**10. Chionolaena latifolia** (Benth.) Baker in Martius, Fl. Bras. 6: 132, tab. 43, fig. 2. 1882. *Leucopholis latifolia* Benth., Hooker's Icon. Pl. vol. 12: 14. 1876. TYPE: Brazil. Rio de Janeiro: Itatiaia, 2,400 m, 9 July 1872, *Glaziou 4841* (holotype, P; isotype, S). Figure 14.

*Chionolaena glomerata* Baker in Martius, Fl. Bras. 6: 130. 1882. SYNTYPES: Brazil. Rio de Janeiro: Itatiaia, 6 July 1871, *Glaziou 4851* (lectotype, selected here, P; photograph ex P in GH); Itatiaia, 9 July 1872, *Glaziou 5896* (excluded here, P).

*Chionolaena breweri* Steyermark & Maguire, Acta Bot. Venez. 14(3): 26, fig. 17. 1984. TYPE: Venezuela. Territorio Federal Amazonas: Depto. Atabapo, Cerro Marahuaca, Cumbre, sección suroriental, vecindades del zanjón, 2,685 m, 3°37′N, 65°21′W, 15 Jan. 1981, *B. Maguire et al. 65587* (holotype, VEN not seen; isotype, NY).

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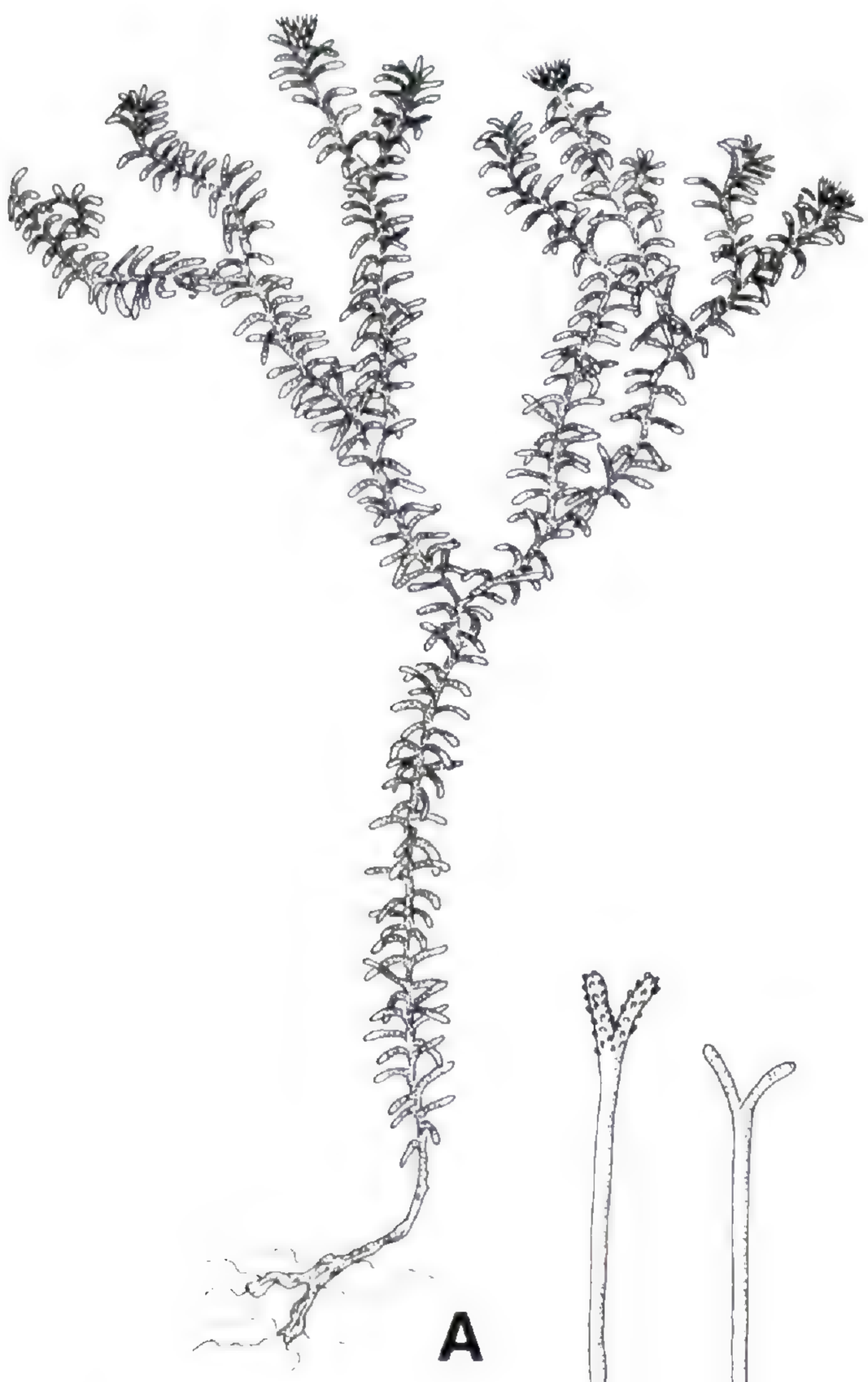
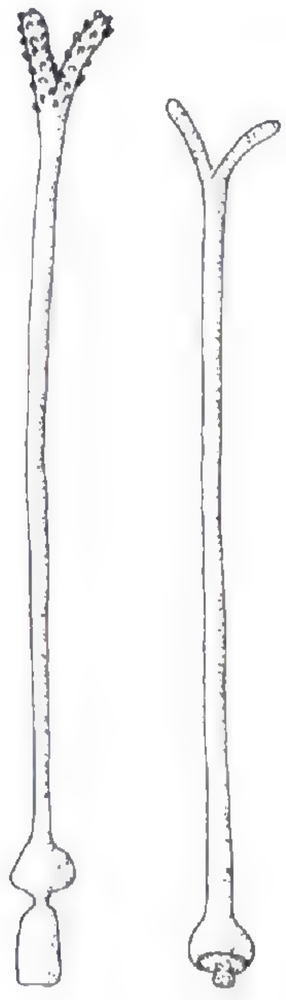
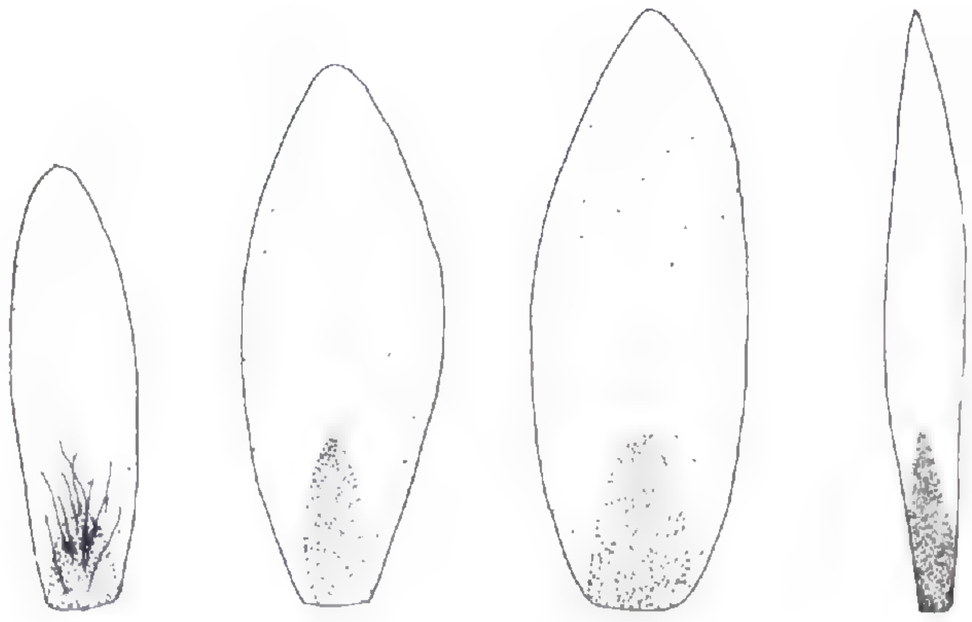
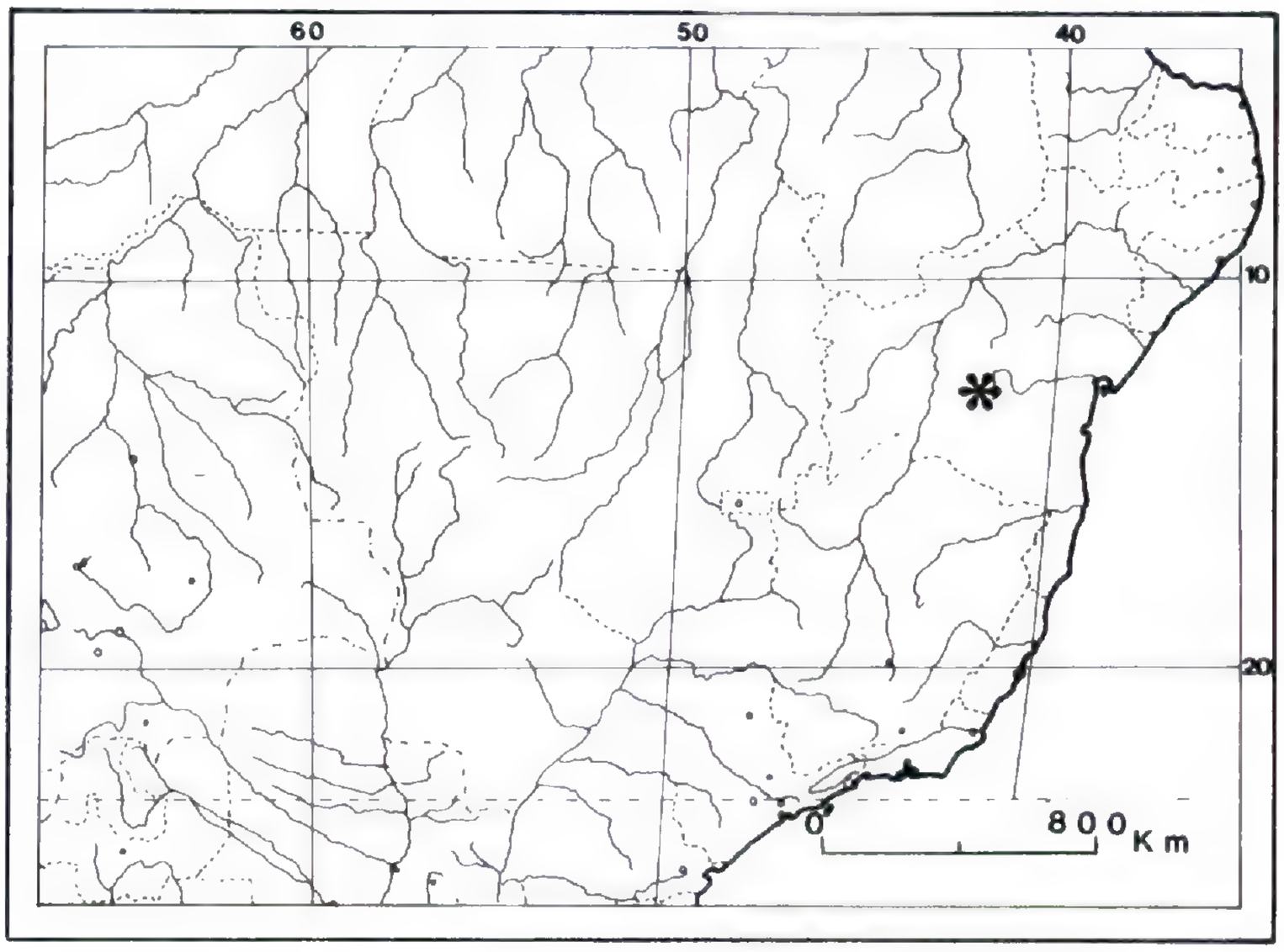
FIGURE 12. *Chionolaena isabellae* Baker in Martius.—A. Habit.—B. Leaf adaxial surface.—C–F. Involucral bracts.—G. Perfect floret.—H. Achene.—I. Stamen. J. Pappus.—K. Style. Below: Brazilian distribution. A–K, *Martinelli et al. 10843* (NY).






A 3 cm

B-C 5 mm

D-G 3 mm

H-I 2 mm

J-N 1 mm

Erect, rigid shrub, moderately branched with densely leafy stems, 15–80 cm high. *Leaves* oblong-elliptic or linear-elliptic, acute, 1.5–4 cm long, 3–5 mm wide with slightly revolute margins, glabrous and bright adaxially, densely lanate and whitish abaxially. *Capitula* heterogamous, arranged in dense umbels, sessile and terminal on the upper branches, these umbels sometimes aggregated corymbosely. *Involucre* narrowly oblong. Involucral bracts 15–21; outer bracts ovate, acuminate, 3–4 mm long, 1–1.5 mm wide; inner bracts linear, subacute, 4–6.5 mm long, 0.5–1 mm wide. *Florets* 5–14, pistillate slightly fewer than the functionally staminate. *Pistillate florets* 2–6; corollas 2–3 mm long; achenes oblong to oblong-elliptic, 0.6–1.2 mm long, 0.2–0.4 mm wide, pubescent with long, apically obtuse, duplex hairs. *Functionally staminate florets* 3–9, corollas 2–3 mm long; style branches truncate, 0.2–0.4 mm long; anthers 0.8–1.3 mm long with tails slightly exceeding or equaling antheropodium; ovaries sterile, oblong, flattened, 0.6–1 mm long, 0.2–0.4 mm wide, pubescence as in pistillate florets.

*Distribution.* *Chionolaena latifolia* grows on open rocky slopes, between 2,300 and 3,000 m. This species has a discontinuous distribution, confined to northern Amazonia and southeastern Brazil. Similar distributions are frequent among other plant species (Harling, 1958; Maas, 1972; Andersson, 1977). Flowering collections were made between October and March.

*Additional specimens examined.* BRAZIL. MINAS GERAIS: Itatiaia, 2,400 m, 10 Jan. 1876, *Glaziou 5903* (cited by Baker for *Chionolaena latifolia*; NY, S); near summit of Mt. Itatiaia, Campo Bello, 3,000 m, 26 Dec. 1916, *O. Ames s.n.* (GH). RIO DE JANEIRO: Itatiaia, Agulhas Negras, 2,600 m, 22–28 Nov. 1938, *Markgraf & Brade 3702* (RB—2 sheets); Agulhas Negras, Mt. Itatiaia, Estação Biologica, 2,300–2,931 m, 22°24′S, 44°41′W, lower slopes, 5 Jan. 1929, *Smith 1682* (GH, US); Serra do Itatiaia, ca. 3,000 m, 27 July 1901, *Hemmendorff 648* (S); ca. 2,200 m, in campo saxoso, 17 Oct. 1903, *Dusén 2007* (S); Sierra da Pedra Asentada, in rupitens, 2,300 m, 30 May 1902, *Dusén 395* (S—2 sheets); Itatiaia, Pedra do Altar, 2,400 m, Mar. 1937, *Brade 15597* (RB—2 sheets); Campo Itatiaia, 13 May 1906, *Luederwaldt 16733* pro parte (US); Municipio Resende, Itatiaia National Parque, planalto of Mt. Itatiaia, 2,400 m, 22°25–26′S, 44°41–42′W, ½–1 km N of shelter house, "Abrigo Rebouças" in valley leading to the rock outcrop, "Pedra do Altar," 3 Nov. 1965, *G. Eiten & L. T. Eiten 6553* (US). VENEZUELA. TERRITORIO FEDERAL AMAZONAS: Depto. Atabapo, Cerro Marahuaca, cumbre, porción suroccidental (Atahua-Shiho), vegetación no arbolada en terreno pendiente, 2,450–2,480 m, 3°30′N, 65°20′W, 9–10 Feb. 1982, *Steyermark, Guariglia, Holmgren & Mori 126322* (paratype of *Chionolaena breweri*, U); extremo noreste, 3°50′N, 65°28′W, 2,580–2,600 m, 30 Mar.–1 Apr. 1983, *Steyermark & F. Delascio 129265* (MO); Cerro Marahuaca-FHUIF, cumbre, zona boscosa en la falda este del riachuelo, 2,480–2,500 m, 3°35′N, 65°20′W, 1–2 Feb. 1982, *Steyermark et al. 126074* (U); Cerro Marahuaca, summit on undulating plateau with islands of shrubs and Marahuaca with stream branch leading to Salto de Monos and SE of summit Camp, 3°37′N, 65°23′W, 2,520–2,650 m, 26–27 Feb. 1985, *Steyermark & Holst 130822* (MO); open rocky plateau of Cerro de Marahuaca above Salto Los Monos on tributary of headwaters of Rio Iguapo, 3°37′N, 65°23′W, 2,555 m, 26 Feb. 1985, *R. L. Liesner 17987* (U).

*Chionolaena latifolia* is an easily recognized species with characteristic foliage, i.e., elliptic leaves with glabrous, bright adaxial surfaces and slightly revolute margins.

Steyermark and Maguire (Steyermark, 1984) described *C. breweri* from Venezuela. This species was said to differ from *C. latifolia* in the width of the capitulescence, size of the capitula, and habit. Because this variation is continuous and not correlated with distribution, these species are treated here as conspecific.

I have excluded the sterile syntype of *Chionolaena glomerata, Glaziou 5896*, from this species and placed it under *C. wittigiana* because of its foliage. This specimen has linear leaves with adaxially tomentose surfaces, whereas the leaves of *C. glomerata* (= *C. latifolia*) are elliptic with glabrous, bright adaxial surfaces.

**11. Chionolaena lavandulifolia** (Kunth) Benth. & Hook. f. ex B. D. Jackson, Index Kew., fasc. I: 516. 1893. *Elichrysum lavandulaefolium* Kunth, Nov. Gen. Sp. ed. fol. IV: 86. 1818. *Gnaphalium lavandulaceum* DC., Prodr. 6: 227. 1837, nom. nov. due to *Gnaphalium lavandulaefolium* Willd. *Chionolaena lavandulaceum* (DC.) Hemsley, Prodr. Biol. Centr. Amer., Bot. 2: 134. 1881, nom. illeg., oldest epithet not used. *Gnaphalium lavandulaefolium* (Kunth) S. F. Blake, Contr.

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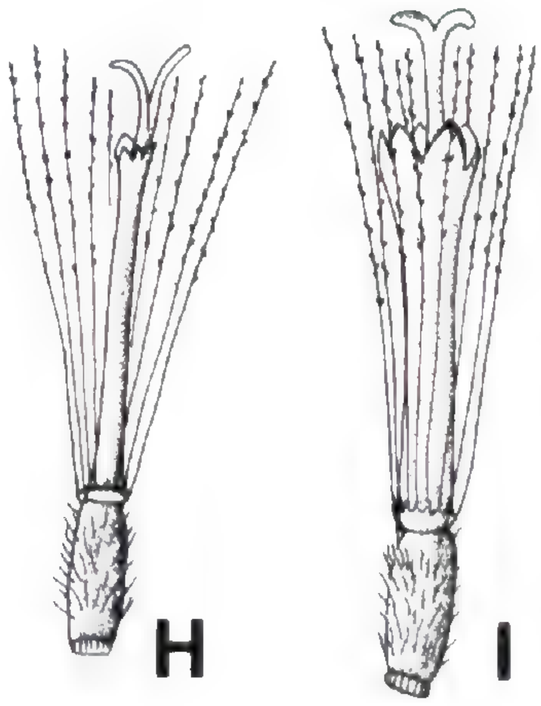
FIGURE 13. *Chionolaena jeffreyi* H. Robinson.—A. Habit.—B, C. Leaves, adaxial surface (left), abaxial surface (right).—D–G. Involucral bracts.—H. Pistillate floret.—I. Functionally staminate floret.—J. Style of functionally staminate floret.—K. Style of pistillate floret.—L. Stamen.—M. Achene of pistillate floret.—N. Ovary of functionally staminate floret. Below: Brazilian distribution. A–N, *Harley et al. 19677* (RB).



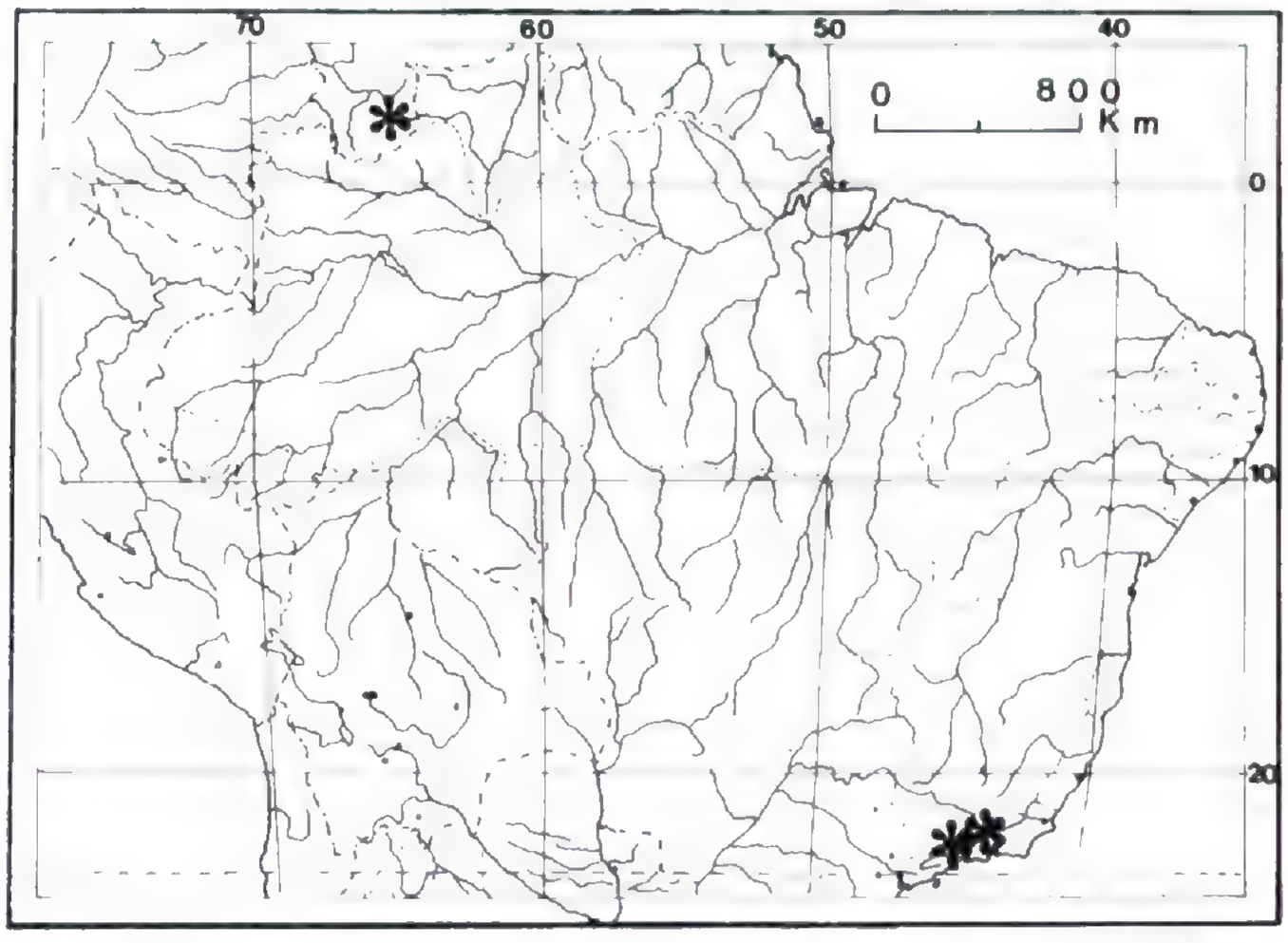
A 3cm

B-C 5mm

D-I 3mm

J-K 2mm

L-N 1mm



Gray Herb. n.s. 52: 21. 1917, hom. illeg., non *Gnaphalium lavandulaefolium* Willd., Sp. Pl. 3: 1868, 1804, which is *Elichrysum lavandulaefolium* (Willd.) D. Don., Mem. Wern. Nat. Hist. Soc. 5: 550, 1826. TYPE: Mexico. Crescit in frigidis Andium Mexicanorum in nobilissimo monte Nauhcampatepetle juxta urbem Perote, alt. 1720 hex. h. Floret Martio Herb. HBK (holotype, P not seen; photograph at GH, LP-neg.no.37976, distributed by F). Figure 15.

Caespitose, multibranched shrub with weakly woody stems, 10–25 cm high. *Leaves* linear-elliptic, acute, 7–18 mm long, 1.5–3.5 mm wide with margins sometimes slightly revolute, tomentose adaxially, densely lanate and whitish abaxially. *Capitula* heterogamous, commonly arranged in dense umbels sessile and terminal on the upper branches, sometimes in a compact corymb. *Involucre* obdeltate. Involucral bracts 25–44; outer bracts broadly ovate, obtuse, 3–4 mm long, 1–2 mm wide, dark brown at the tip; inner bracts linear-oblong, obtuse, 6.5–9 mm long, 0.5–1 mm wide, dark brown above the stereome. *Florets* 11–48, pistillate more numerous or slightly more numerous than the functionally staminate, sometimes slightly fewer than the functionally staminate. *Pistillate florets* 6–24; corollas 3–4.5 mm long; achenes oblong elliptical, 0.7–1.9 mm long, 0.3–0.6 mm wide, glabrous, occasionally shortly pubescent with apically obtuse, duplex hairs. *Functionally staminate florets* 5–13; corollas 3–5 mm long; style branches rounded or subacute, 0.2–0.4 mm long; anthers 1.5–2.2 mm long with tails shorter than anther-opodium; ovaries sterile, flattened, 0.25–0.70 mm long, 0.1–0.4 mm wide, glabrous, occasionally with short pubescence as in pistillate florets. Pappus bristles with apical cells slightly swollen and acute at the apex.

*Distribution.* *Chionolaena lavandulifolia* has a highly disjunct distribution, i.e., it occurs in the central mountains of Mexico and in the central parts of Costa Rica. This species is found among rocks in sandy, gravelly soil and volcanic sand on open exposures, commonly on summits between 3,150 and 4,200 m. Flowering collections were made between July and March, except in November and December.

*Additional specimens examined.* MEXICO. MEXICO: summit ledges, Nevado de Toluca, 2 Sep. 1882, *Pringle 4223* (M, UC); Nevado de Toluca, Alpine Region, 4,000 m, 27 Mar. 1954, *Troll 721* (M); Ixtaccihuatl, S side of mtn. at La Joya, ca. 4,015 m, "in crevices at base of cliff, occasional," 8 Aug. 1960, *Beaman 3511* (UC); 4,000 4,050 m, "under rock ledge," 30 July 1958, *Beaman 1961* (UC); La Joya de Alcalican, extremo SW del Ixtaccihuatl, municipio de Amecameca, "pradera alpina," 3,900 m, 13 Nov. 1977, *Rzedowski 35551* (UC); Ixtaccihuatl, 12,000 13,000 ft., Sep.—Oct. 1905, *Purpus 1523* (UC). PUEBLA: Mt. Orizaba, rocks, alpine region, Mar. 1908, *Purpus 2990* (UC); Orizaba, 3,800–4,200 m, Oct. 1906, *Ross 1265* (HBG, M); Mount, 13,300 ft., rocks and volcanic sand open exposures, 29 July 1928, *Balls B5139* (UC). VERACRUZ: Cofre de Perote, summit of mtn., 4,192 m, 6 Mar. 1958, *Beaman 2145* (UC). COSTA RICA. On rocky ground on lower slope of Cerro Frio, Buenavista massif, 3,400 m, 14–16 Mar. 1969, *Weston 5877* (UC); Rochers de la region superieure du Cerro de Buena Vista, 19 Jan. 1891, *Pittier 3430* (G); Cerro de La Muerte region, Cordillera de Talamanca, near summit of Cerro Sakira, 3,415 m, 8 Jan. 1985, *Horn 38* (UC); Chirripó Grande, 3,450 m, 29 Apr. 1932, *Kupper 1301a* (M), 27 Apr. 1932, *Kupper 1301* (M), 28 Apr. 1932, *Kupper 1148* (M); below Sabana Chirripó, Chirripó massif, 3,150 m, 24 Feb. 1976, *Weston 10122* (UC); Cerro de Chirriposillo (Cuericil) within ca. 200 m of main summit, 3,400 m, 2 Mar. 1964, *Weston 1551* (UC); Prov. of Cartago, shrub-paramo (*Chusquea*, *Hypericum*, *Vaccinium*), Cerro de La Muerte, Pan-American highway, 5 km above Millsville (about 8 km above Nivel), Cordillera de Talamanca, 3,400–3,500 m, crevice in rocks, common at summit, characteristic together with caespitose *Hypericum* of rocky high paramo, 25 July 1949, *R. W. Holm & H. H. Iltis 573* (M); in summo monte Irazu, Jan. 1847, *Oersted 10570* (GH, MO, UC).

*Chionolaena lavandulifolia* is closely related to *C. aecidiocephala*. In both species the outer bracts are obtuse and the capitula are arranged in dense umbels, but the former is easily distinguished by its adaxially densely lanate, linear-elliptic leaves, and commonly glabrous achenes.

**12. Chionolaena lychnophorioides** Sch.-Bip., Pollichia 20–21: 391. 1863. SYNTYPES: Brazil. *Sellow s.n.* (in B presumably lost); *Riedel*

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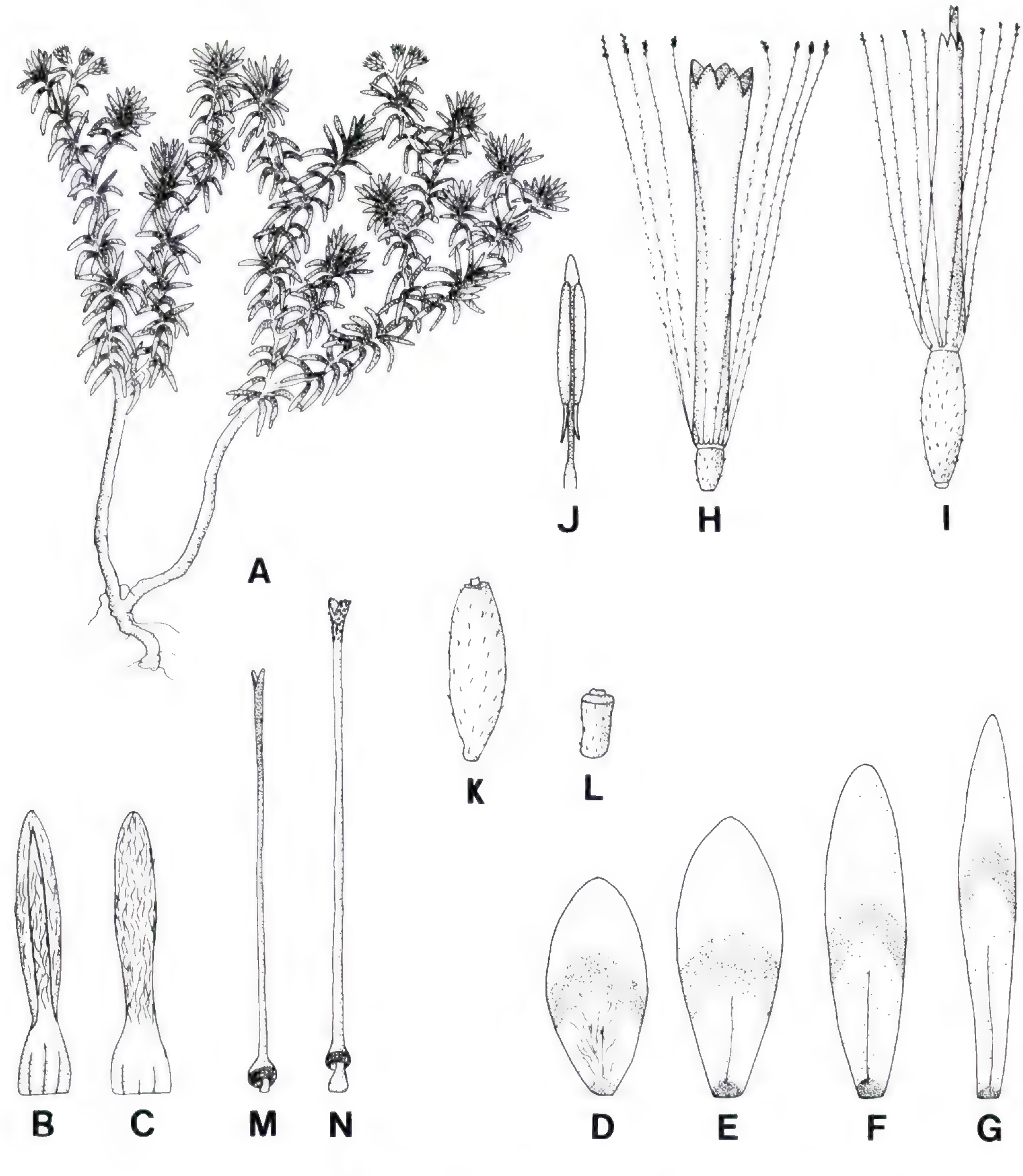
FIGURE 14. *Chionolaena latifolia* (Benth.) Baker in Martius.—A. Habit.—B, C. Leaves, adaxial surface (left), abaxial surface (right).—D–G. Involucral bracts.—H. Pistillate floret.—I. Functionally staminate floret.—J. Style of pistillate floret.—K. Style of functionally staminate floret.—L. Stamen.—M. Achene of pistillate floret.—N. Ovary of functionally staminate floret. Below: northern Amazonian (Venezuela) and Brazilian distribution. A–N, *Smith 1682* (GH).



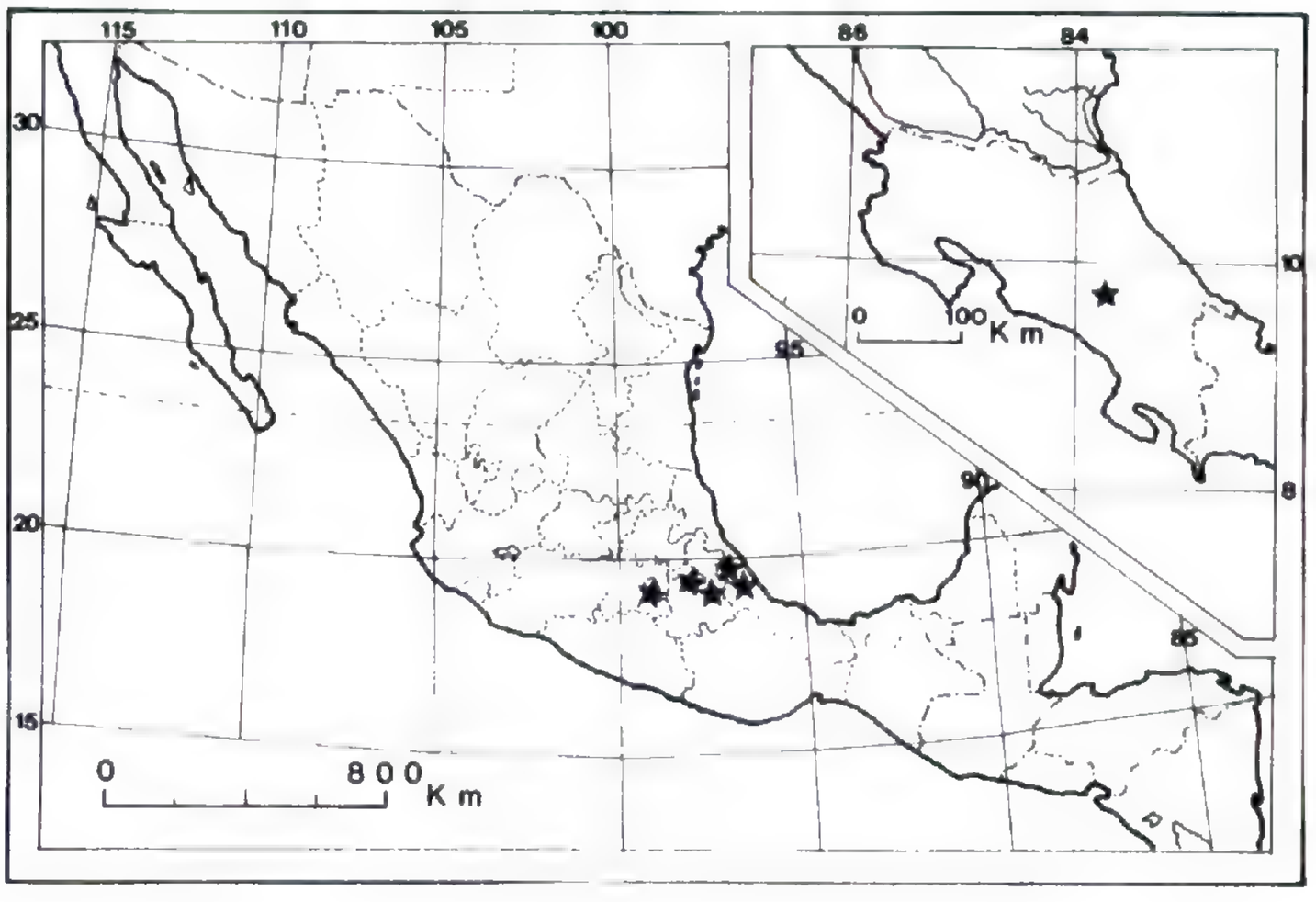

A 3 cm

B-C 1 cm

D-G 3 mm

H-I 3 mm

J-N 2 mm



*s.n.* (in rocky area on Itacolumy mountain, Aug. 1824, LE not located); *Claussen 184* (Minas Gerais, Crarassa, lectotype, selected here, P; negative at LP). Figure 16.

Erect, rigid shrub, moderately branched, 15–35 cm high. *Leaves* linear, acute, 1.3–3.3 cm long, 1.2–3 mm wide with slightly revolute margins, adaxially arachnoid pubescent, densely lanate and whitish abaxially. *Capitula* heterogamous, solitary on the upper branches, occasionally arranged in terminal, small, loose umbels at the ends of the leafy stems. *Involucre* broadly campanulate. Involucral bracts 28–29; outer bracts linear ovate, acute, 5 mm long, 1–1.5 mm wide; inner bracts linear, 5–6 mm long, 0.9 mm wide. *Florets* 48–54, pistillate more numerous than the functionally staminate. *Pistillate florets* ca. 35; corollas 2–2.5 mm long; achenes oblong, 1–3 mm long, 0.3–1.2 mm wide, pubescent with long, apically acute, duplex hairs. *Functionally staminate florets* ca. 13; corollas 3.5–4 mm long; style branches acute or rounded, 0–0.4 mm long; anthers 1.5–1.7 mm long with tails equaling antheropodium; ovaries sterile.

*Distribution.* *Chionolaena lychnophorioides* is restricted to the state of Minas Gerais in southeastern Brazil. It occurs in the planalto, which has a temperate climate and well-marked dry season. This species grows on stony and rocky mountain slopes, between 1,350 and 1,450 m. Flowering collections were made in April, May, and December.

*Additional specimens examined.* BRAZIL. MINAS GERAIS: Itacolumy Ouro Preto, 7 July 1884, *Glaziou 14960a* (MO, US); Itacolumy (E of Ouro Preto), 8 Apr. 1925, *Chase 9389* (GH, MO); Itacolumy, Feb. 1892, *Ule 2601* (HBG); Itacolumy, Ouro Preto "campestre da serra," 28 Dec. 1950, *A. Macedo 2801* (NY, RB, US); Pico Itambe, depressao, terreno (valo) no alto Serra, 5 May 1942, *M. Magalhaes 1696* (COL); Serra de Ibitipoca, Pico do Piao, 1,350 1,450 m, formações de arenito de Serie Lauras, 14 May 1970, *Sucre & Krieger 6836* (RB).

*Chionolaena lychnophorioides* is distinguished by its usually solitary capitula with numerous florets and its linear leaves. It is related to *C. arbuscula*, from which it is readily distinguished by its broadly linear leaves with slightly revolute margins and capitula with pistillate florets outnumbering the functionally staminate florets.

**13. Chionolaena mexicana** Freire, sp. nov. TYPE: Mexico. Hidalgo: Sierra de Pachuca, 10,000 ft., 20 Feb. 1899, *Pringle 7700* (holotype, K). Figure 17.

*Frutex* erectus dichotome ramosus, usque ad ca. 0.3 m altus. Caules ascendente-erecti, tomentosi, foliati, vetustiores glabri nudi, cicatricibus foliorum notati. *Folia* alterna, suberecto-patentia, inferiora deflexa, obovata, obtusa, 15–25 mm longa, 3–7 mm lata, apice mucronata, margine revoluta, supra tomentosa, subtus dense et persistenter incana. *Corymbi* terminales. *Capitula* heterogama. Involucrum campanulatum. Bracteae involucri 34 36, exteriores ovatae, interiores lineares, lamina alba. Flores 25–26, albidi in apicibus rosei. *Flores radii* 14–15, feminei, fertiles. Corollae filiforme-bilabiatae ca. 3.8 mm longae. Stilus bifidus. Achenia oblonga, ca. 1 mm longa, ca. 0.3 mm lata, minute puberula. *Flores disci* ca. 11, hermaphroditi, steriles et masculae fungentes. Corollae tubulosae, 5-lobatae, ca. 4 mm longae. Stylus bifidus, ramis apice truncatis et dorso pubescentibus. Antherae ca. 1.8 mm longae, caudae antherarum ca. 0.3 mm longae. Achenia sterilia, anguste oblonga. Pappus albus, uniserialis, setis scabris corolla parum longioribus, barbellatis, basi in annulo concretae formantes, florum tubulosarum apice incrassatis.

Erect, dichotomously branched, rigid shrub, 30 cm high. *Leaves* narrowly obovate, slightly attenuate at the base, obtuse, 1.5–2.5 cm long, 3–7 mm wide with slightly revolute margins, tomentose adaxially, densely whitish lanate abaxially. *Capitula* heterogamous, 10–18, arranged in corymbs sessile and terminal on the upper branches. *Involucre* obdeltate. Involucral bracts 34–36; outer bracts ovate, slightly acuminate, 2.2–2.5 mm long, 1 mm wide; inner bracts linear, obtuse, 5–6.5 mm long, 0.5 mm wide, dark above the stereome. *Florets* 25–26, pistillate slightly more numerous than the functionally staminate. *Pistillate florets* 14–15; corollas 3.8 mm long; achenes oblong, 1 mm long, 0.3 mm wide, pubescent with short, apically obtuse, duplex hairs. *Functionally staminate florets* ca. 11; corollas 4 mm long; style branches truncate, 0.4 mm long; anthers 1.8 mm long with tails slightly shorter than antheropodium; ovary sterile, flattened, 0.7 mm long, 0.2 mm wide, pubescence as in pistillate florets.

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FIGURE 15. *Chionolaena lavandulifolia* (Kunth) Benth. & Hook. f. ex B. D. Jackson. —A. Habit. —B, C. Leaves, abaxial surface (left), adaxial surface (right). —D–G. Involucral bracts. —H. Functionally staminate floret. —I. Pistillate floret. —J. Stamen. —K. Achene of pistillate floret. —L. Ovary of functionally staminate floret. —M. Style of pistillate floret. —N. Style of functionally staminate floret. Below: Mexican and Central American (Costa Rica) distribution. A–N, *Gonzalo Flores M. PV78120* (UC).

*Distribution.* Known only from the type collection, the state of Hidalgo, Sierra de Pachuca at 2,700 m. A flowering collection was made in February.

This species is readily distinguished from all other species of *Chionolaena* by its obovate leaves, corymbosely arranged heterogamous capitula, and achenes with obtuse short hairs. Its closest relative appears to be *C. concinna*, the only other Mexican species with obovate leaves, capitula arranged in corymbs, and achenes with obtuse short hairs. *Chionolaena mexicana* differs from *C. concinna* by its erect, rigid habit, and capitulescence terminal at maturity. In addition, the leaves of *C. concinna* are narrowed into a petiolariform base. In *C. mexicana*, the leaves are basally attenuate.

**14. Chionolaena phylicoides** (Gardner) Baker in Martius, Fl. Bras. 6: 131. 1882. *Leucopholis phylicoides* Gardner, London J. Bot. 2: 11. 1843. TYPE: Brazil. Rio de Janeiro: Organ Mountains, 1836–1841, *Gardner 5772* (lectotype, selected here, GH, photograph at LP; isolectotypes, G—3 sheets, NY, S). Figure 18.

Erect, rigid shrub, moderately branched with stems densely leafy, 15–45 cm high. *Leaves* oblong, acute, 5–10 mm long, 1–2 mm wide, glabrous and bright adaxially, densely woolly and completely concealed by the revolute margins abaxially. *Capitula* homogamous, unisexual, arranged in dense umbels sessile and terminal on the upper branches. *Involucre* narrowly oblong. Involucral bracts 20–30; outer bracts linear ovate, acuminate, 4–5 mm long, 1 mm wide; inner bracts linear, obtuse, 4–5 mm long, 0.7–0.8 mm wide. *Florets* 7–12, all hermaphroditic functionally staminate florets with ovary not developed, functionally pistillate florets without anthers. *Functionally pistillate florets* ca. 10; corollas 3  3.8 mm long.; style branches truncate, 0.4–1 mm long; anthers 0; achenes oblong, 0.8–0.9 mm long, 0.2–0.5 mm wide, pubescent with long, duplex hairs obtuse at the tip. *Functionally staminate florets* 7–12; corollas 2–3.5 mm long; style branches truncate, 0–0.5 mm long; anthers 5, 1.2–1.8 mm long with tails equaling antheropodium; ovaries sterile, flattened, 0.5 0.8 mm long, 0.15–0.40 mm wide, pubescence as in pistillate florets.

*Distribution.* Restricted to the states of Minas Gerais and Rio de Janeiro in southeastern Brazil where a slightly marked dry season occurs. This species grows commonly in rocky places on hillsides beween 1,950 and 2,850 m. Flowering collections were made between June and November.

*Additional specimens examined.* BRAZIL. MINAS GERAIS: 3 Nov. 1887, *Glaziou 16157* (G, NY); Serra do Caparaó, Pico do Calçado, 2,850 m, 25 Sep. 1941, *Brade 17012* (NY); Pico do Cristal, 2,600 m, 24 Oct. 1941, *Brade 17004* (NY). RIO DE JANEIRO: Serra dos Orgãos, Oct. 1958, *Schnell 8432* (RB); Campo das Antas, 31 July 1940, *Brade 16517* (GH, NY), 30 Jan. 1942, *Pereira 208* (NY, RB); 2,000 m, *Rizzini*, 5 June 1951, (RB 73702 pro parte); Felsen, 1,950 m, Oct. 1952, *Markgraf 10102* (NY, RB pro parte); Caminho para o Campo das Antas, 1 Nov. 1970, *Equipe do Projecto Serra dos Orgãos* (RB); Centralstock, 2,400–2,600 m, Aug. 1915, *Luetzelburg 6252a, b, 6386* (both M); Municipio de Teresópolis, Parque Nacional de Serra dos Orgãos, Campo das Antas, 1,800–2,000 m, 1 Feb. 1983, *Martinelli & Simonis 9051* (US), *Dionisio & Octavio*, 28 June 1942 (RB); Municipio de Petropólis, Correiras, Picada para o Açú, Campos de Altitude em direção do Morro da Bandeira, 2,000 2,100 m, crescendo em ilhas formadas com Melastomataceae, *Prepusa* sp., Gramineas, Cyperaceas, *Farney, E. C. Dalcin & Pena 800* (RB); Haut des Orgues, 1885, *Glaziou 14961* (G). WITHOUT STATE: "Minas Claparao," *O. Voll.*, 2 Jan. 1937 (RB); Pedra do Sino, 1,750 m, rara no Parque, 17 Sep. 1948, *Rizzini 368* (RB). WITHOUT LOCATION: "turberas con *Sphagnum*," *Cabrera 12227* (LP).

*Chionolaena phylicoides* is closely related to *C. chrysocoma*. In both species the capitula are arranged in umbels and the abaxial leaf surfaces

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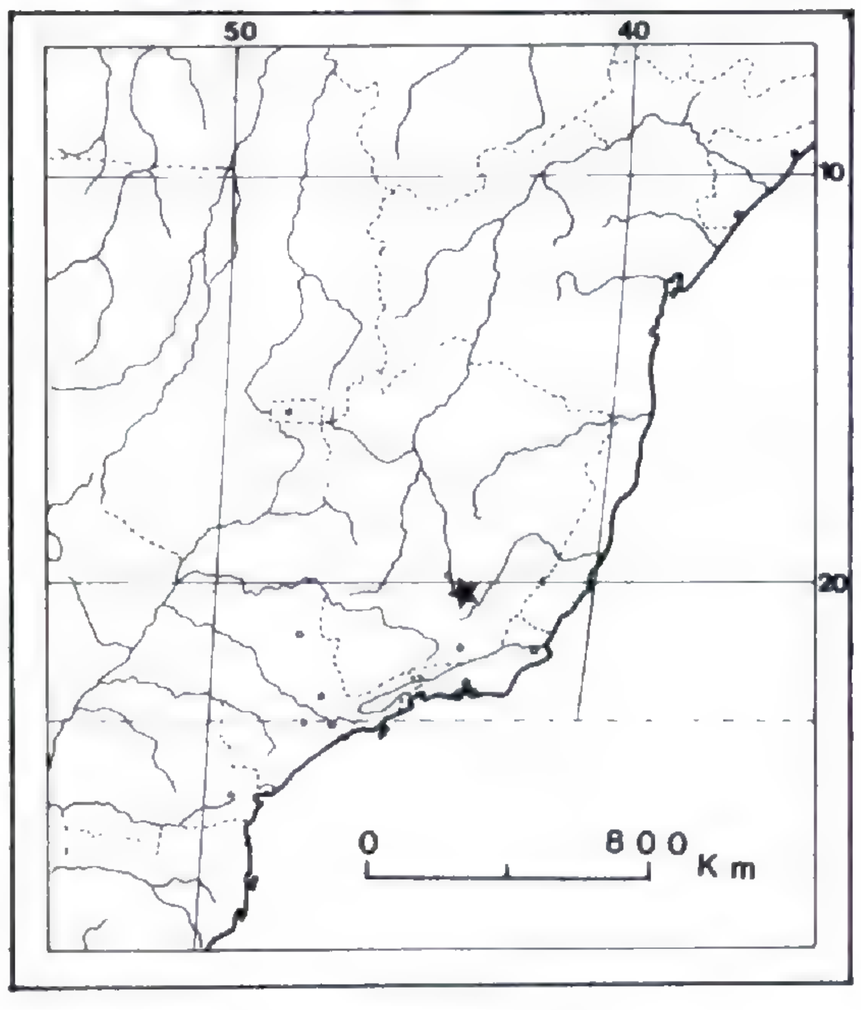
FIGURE 16. *Chionolaena lychnophorioides* Sch.-Bip.—A. Habit.—B, C. Leaves, adaxial surface (left), abaxial surface (right).—D G. Involucral bracts.—H. Pistillate floret. I. Functionally staminate floret.—J. Style of pistillate floret.—K. Style of functionally staminate floret.—L. Achene of pistillate floret. M. Summit of pistillate corolla.—N. Stamen. Below: Brazilian distribution. A N, *Chase 9389* (MO).

FIGURE 17. *Chionolaena mexicana* Freire. A. Habit.—B. Leaf abaxial surface.—C–F. Involucral bracts.—G. Pistillate floret.—H. Functionally staminate floret.—I. Stamen.—J. Style of pistillate floret.—K. Style of functionally staminate floret. -L. Achene of pistillate floret. M. Ovary of functionally staminate floret. Below: Mexican distribution. A–M, *Pringle 7700* (K).

FIGURE 18. *Chionolaena phylicoides* (Gardner) Baker in Martius.—A. Portion of plant.—B, C. Leaves, adaxial surface (left), abaxial surface (right).—D–G. Involucral bracts.—H. Functionally pistillate floret from homogamous capitulum.—I. Style. J. Achene. Below: Brazilian distribution. A J, *Glaziou 16157* (NY).







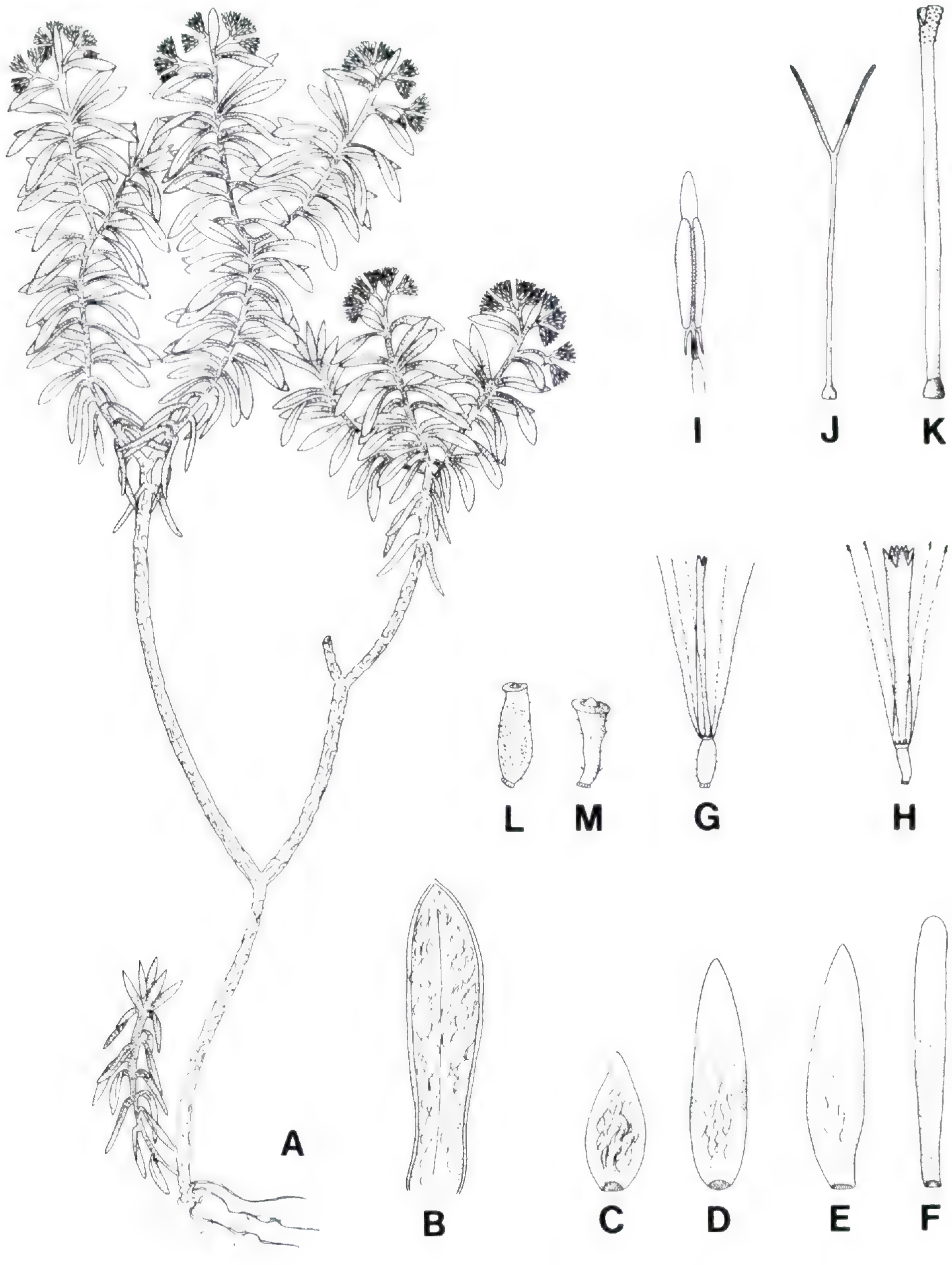
A 3 cm

B·C 1 cm

D·G 5 mm

H·I 3 mm

J·N 2 mm

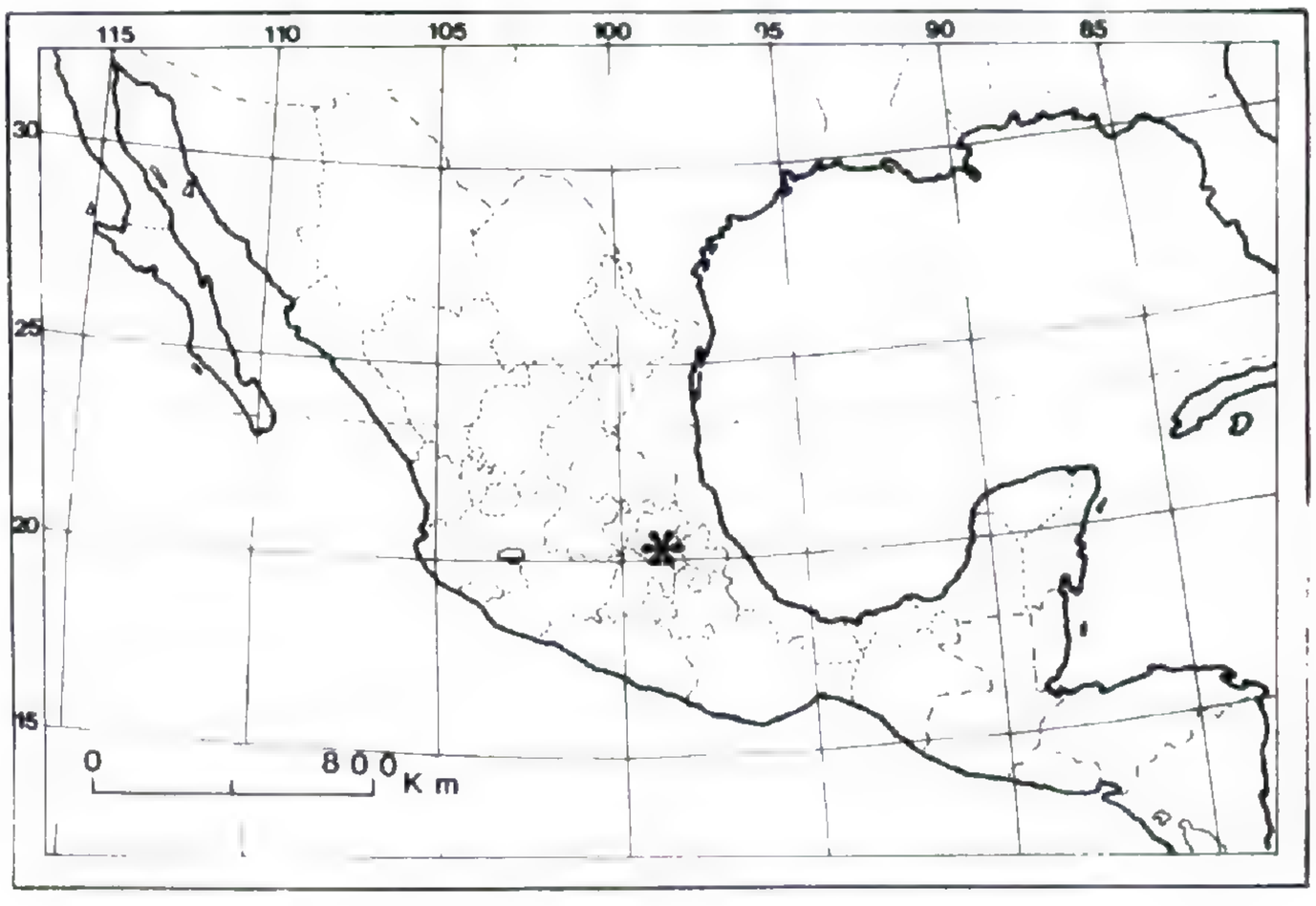


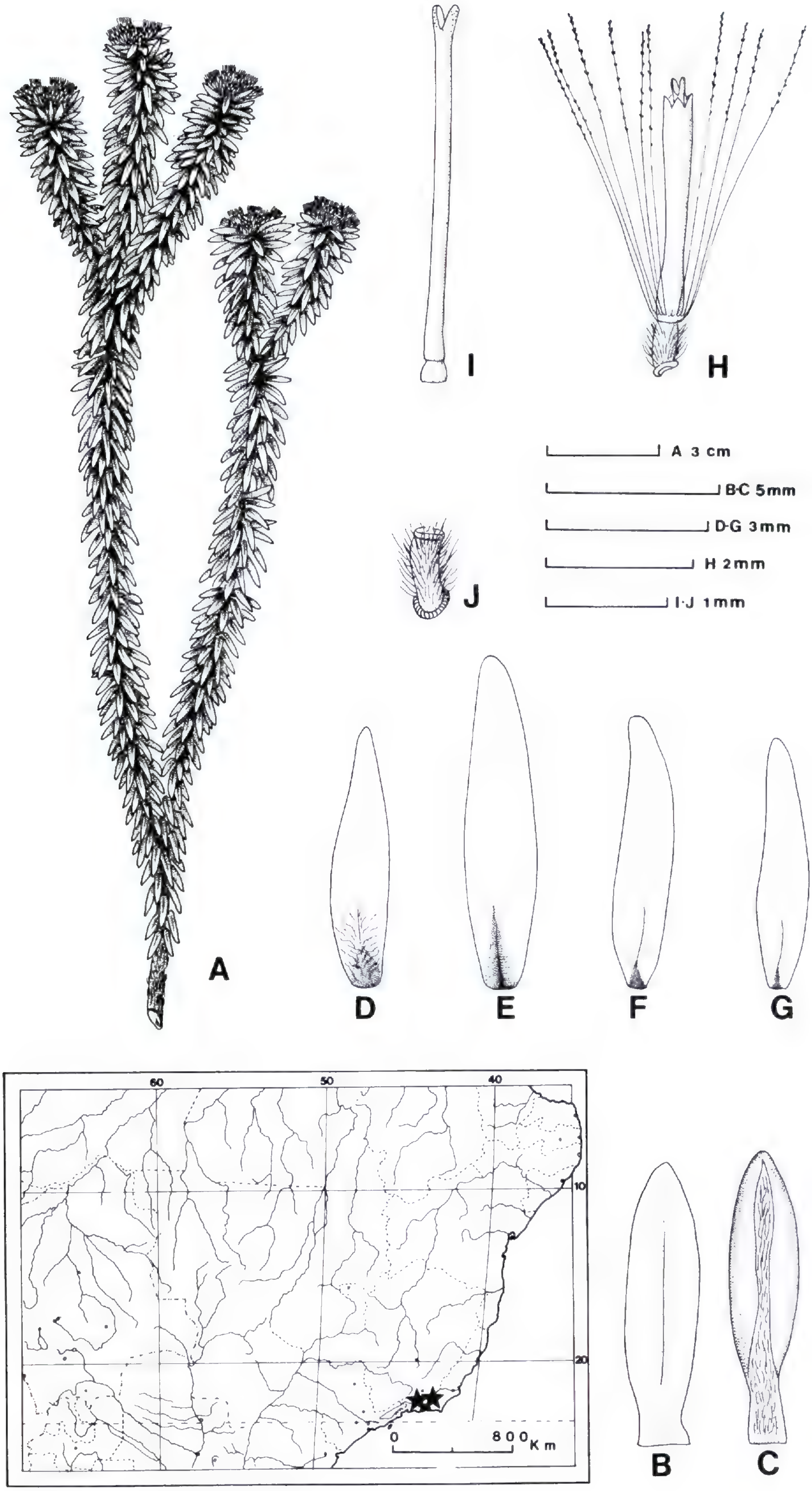

A 3 cm

B 1 cm

C-H 2 mm

I-M 1 mm




A
B
C
D
E
F
G
H
I
J
A 3 cm
B-C 5mm
D-G 3mm
H 2mm
I-J 1mm
60
50
40
10
20
0
800 Km

are completely concealed by the revolute margins. *Chionolaena phylicoides* is, however, distinguished by its homogamous capitula and reflexed leaves.

**15. Chionolaena sartorii** Klatt, Leopoldina 23: 89. 1887. *Gnaphalium sartorii* Sch.-Bip. ex Klatt, Leopoldina 23: 89. 1887, prosyn. sub. *C. sartorii*, nomen nudum. *Gnaphalium sartorii* (Klatt) F. J. Espinosa-Garcia, Bol. Soc. Bot. México 45: 21. 1984. TYPE: Mexico. Sempoaltepec, June 1942, *Liebman 308* (holotype, C; isotype (fragment), GH). Figure 19.

Caespitose subshrub with weakly woody stems, 8–10 cm high. *Leaves* narrowly linear, acute, 1–2 cm long, 1 mm wide with slightly revolute margins, tomentose adaxially, densely whitish lanate abaxially. *Capitula* heterogamous, 3–4, arranged in corymbs sessile and terminal on the upper branches. *Involucre* obdeltate. Involucral bracts 20–25; outer bracts narrowly ovate, acuminate, 3 mm long, 1–1.2 mm wide; inner bracts linear, subacute, 5.5–6 mm long, 0.5 mm wide. *Florets* ca. 20–21, pistillate more numerous than functionally staminate. *Pistillate florets* 14–15; corollas 4 mm long; achenes oblong 0.8 mm long, 0.3 mm wide, pubescent with short, apically obtuse, duplex hairs. *Functionally staminate florets* ca. 6; corollas 4 mm long; style branches rounded, 0.2 mm long; anthers 1.8 mm long with tails equaling or slightly exceeding antheropodium; ovaries sterile, 0.8 mm long, 0.3 mm wide, pubescence as in pistillate florets.

*Distribution.* Known only from the type locality in Sempoaltepec, Mexico, at about 3,300 m. The flowering collection was made in June.

*Chionolaena sartorii* is recognized by its caespitose habit, linear leaves, acute inner bracts, and few, corymbosely arranged capitula.

**16. Chionolaena seemannii** (Sch.-Bip. in Seemann) Freire, comb. nov. *Gnaphalium seemannii* Sch.-Bip. in Seemann, Bot. Voy. "Herald" 7–8: 309. 1856. TYPE: Mexico. Sierra Madre, NW Mexico, *Seemann 1994* (holotype, K). Figure 20.

*Chionolaena corymbosa* Hemsley, Diagn. Pl. Nov. 2: 32. 1879. Nomen superfluum. TYPE: Mexico. Sierra Madre, NW Mexico, *Seemann 1994*.

Woody, rigid shrub with ascendent, erect and densely leafy branches, 15–20 cm high. Stems subdichotomously branched. *Leaves* linear elliptic, acute, 3.5–4.5 cm long, 4–5 mm wide with slightly revolute margins, glabrous adaxially, densely whitish lanate abaxially. *Capitula* heterogamous, up to 10, arranged in primary terminal, sessile corymbs becoming lateral later in development. *Involucre* broadly campanulate. Involucral bracts ca. 38, dark toward middle; outer bracts ovate, obtuse, 4 mm long, 2 mm wide; inner bracts 6 mm long, 0.5 mm wide. *Florets* ca. 84, pistillate much more numerous than the functionally staminate. *Pistillate* florets ca. 70; corollas 3.5 mm long; achenes elliptic, 0.7 mm long, 0.3 mm wide, pubescent with short, apically obtuse, duplex hairs. *Functionally staminate florets* ca. 14; corollas 3.5–3.8 mm long; style branches truncate, 0.4 mm long; anthers 2 mm long with tails slightly exceeding antheropodium; ovary sterile, oblong, flattened, 0.5 mm long, 0.2 mm wide, pubescence as in pistillate florets.

*Distribution.* Known only from the type locality, Sierra Madre, Mexico. No flowering data are available.

*Chionolaena seemannii* is recognized by its corymbosely arranged, broadly campanulate capitula, long linear leaves, and subdichotomously branched stems.

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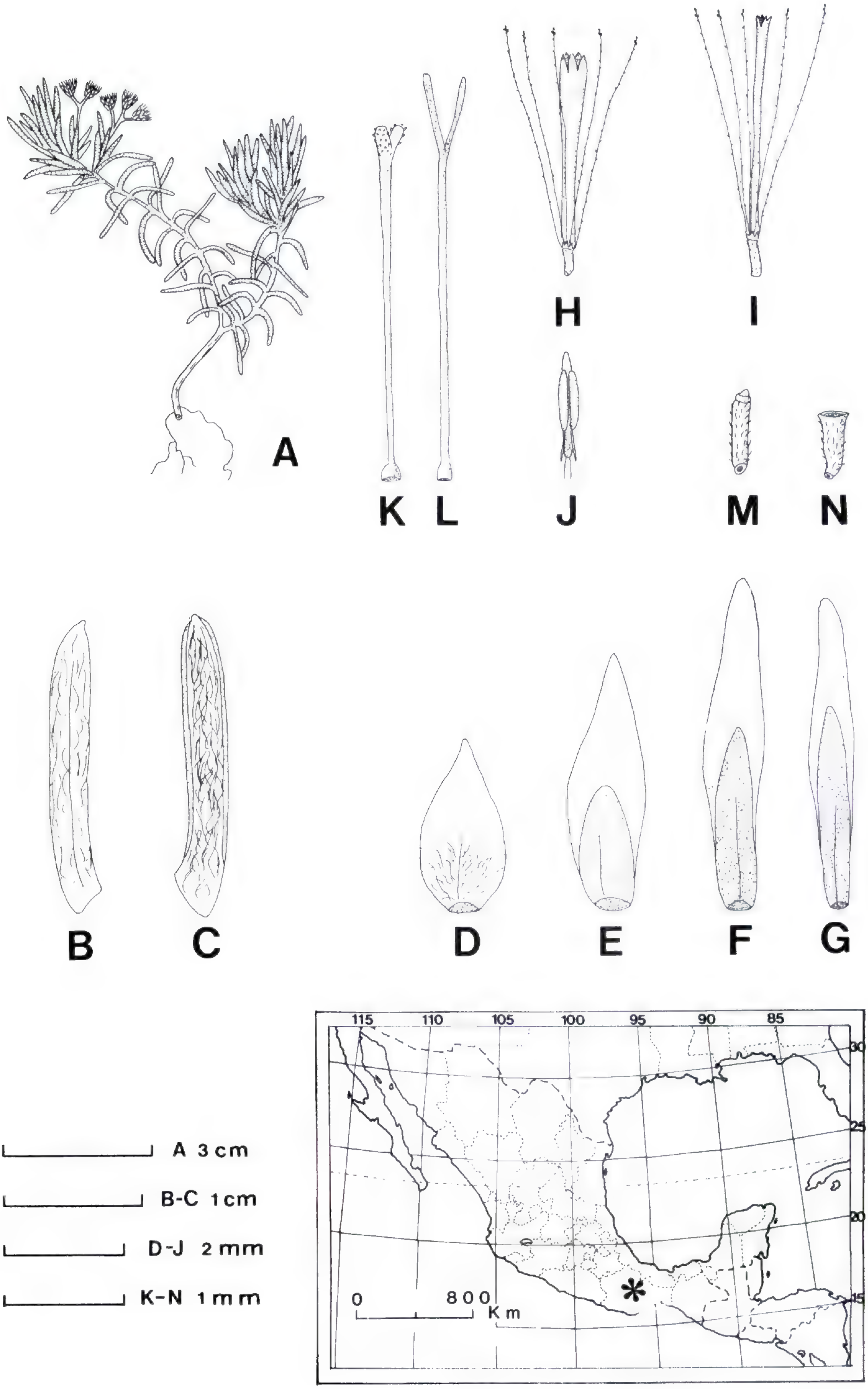
FIGURE 19. *Chionolaena sartorii* Klatt. —A. Habit. —B, C. Leaves, adaxial surface (left), abaxial surface (right). —D–G. Involucral bracts. H. Functionally staminate floret. —I. Pistillate floret. —J. Stamen. —K. Style of functionally staminate floret. L. Style of pistillate floret. —M. Achene of pistillate floret. N. Ovary of functionally staminate floret. Below: Mexican distribution. A–N, *Liebman 308* (C).

FIGURE 20. *Chionolaena seemannii* (Sch. Bip. in Seemann) Freire. —A. Portion of plant. —B. Leaf abaxial surface. —C–F. Involucral bracts. —G. Pistillate floret. —H. Functionally staminate floret. —I. Stamen. —J. Style of pistillate floret. —K. Style of functionally staminate floret. —L. Achene of pistillate floret. —M. Ovary of functionally staminate floret. Below: Mexican distribution. A–M, *Seemann 1994* (K).

FIGURE 21. *Chionolaena wittigiana* Baker in Martius. A. Portion of plant. —B, C. Leaves, adaxial surface (left), abaxial surface (right). —D–G. Involucral bracts. —H. Pistillate floret. —I. Functionally staminate floret. —J. Stamen. K. Style of pistillate floret. —L. Style of functionally staminate floret. —M. Achene of pistillate floret. —N. Ovary of functionally staminate floret. —O. Summit of pistillate corolla. Below: Brazilian distribution. A–O, *Dusén E132* (S).


A
K
L
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D
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A 3 cm
B-C 1 cm
D-J 2 mm
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115
110
105
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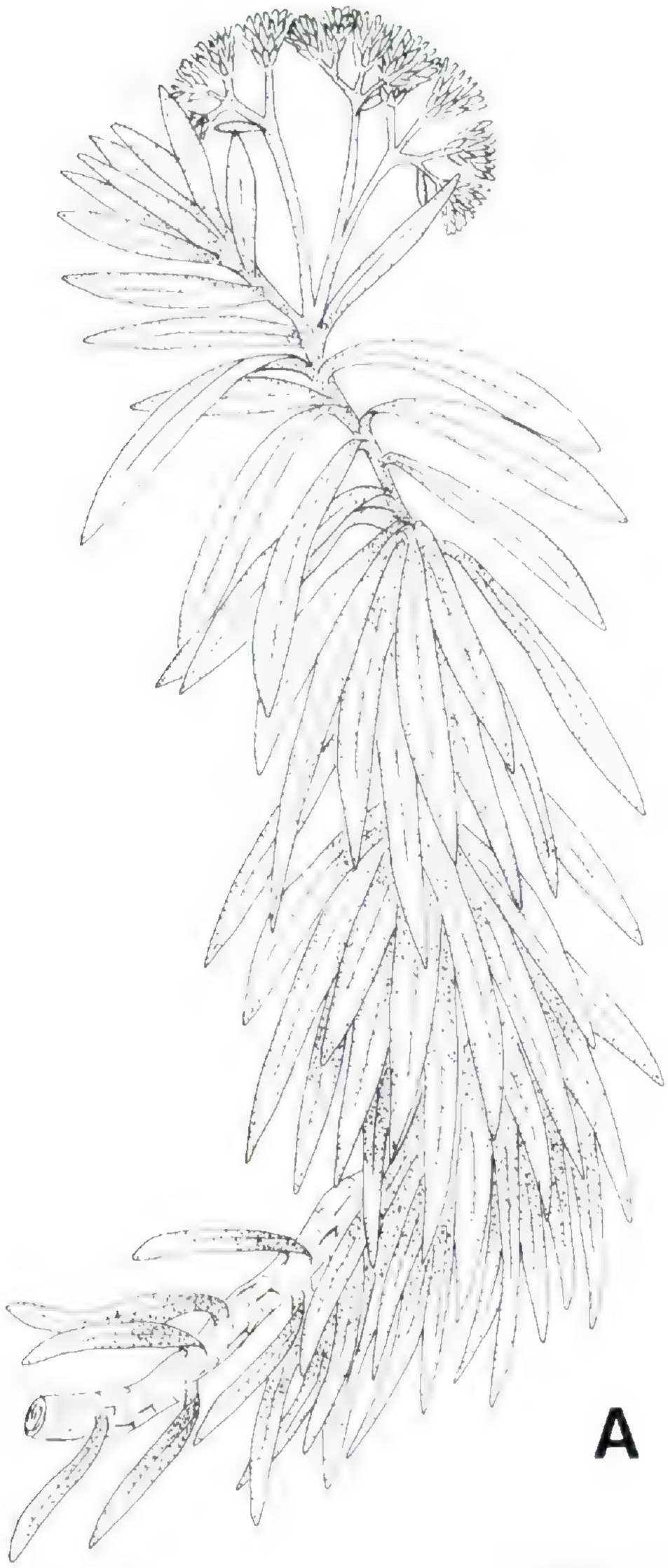
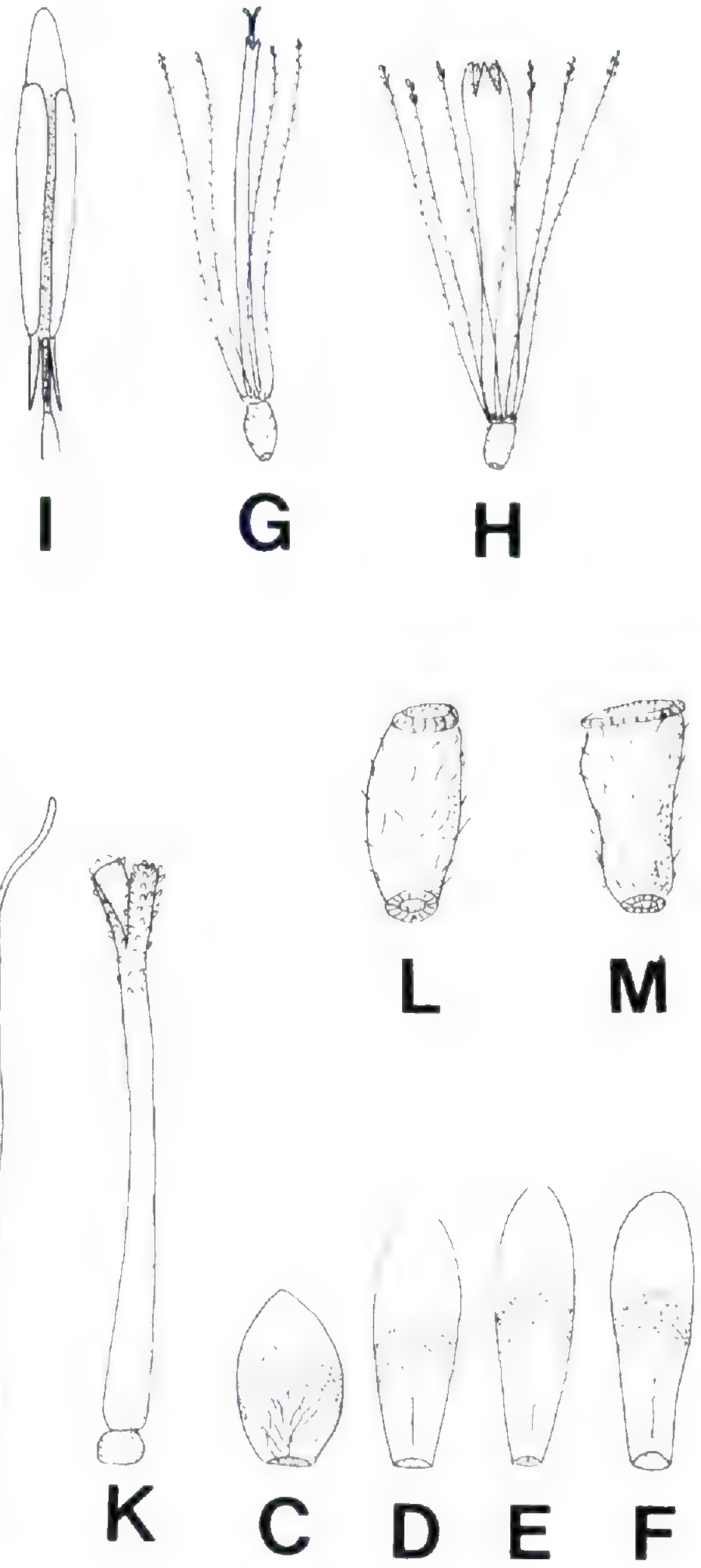
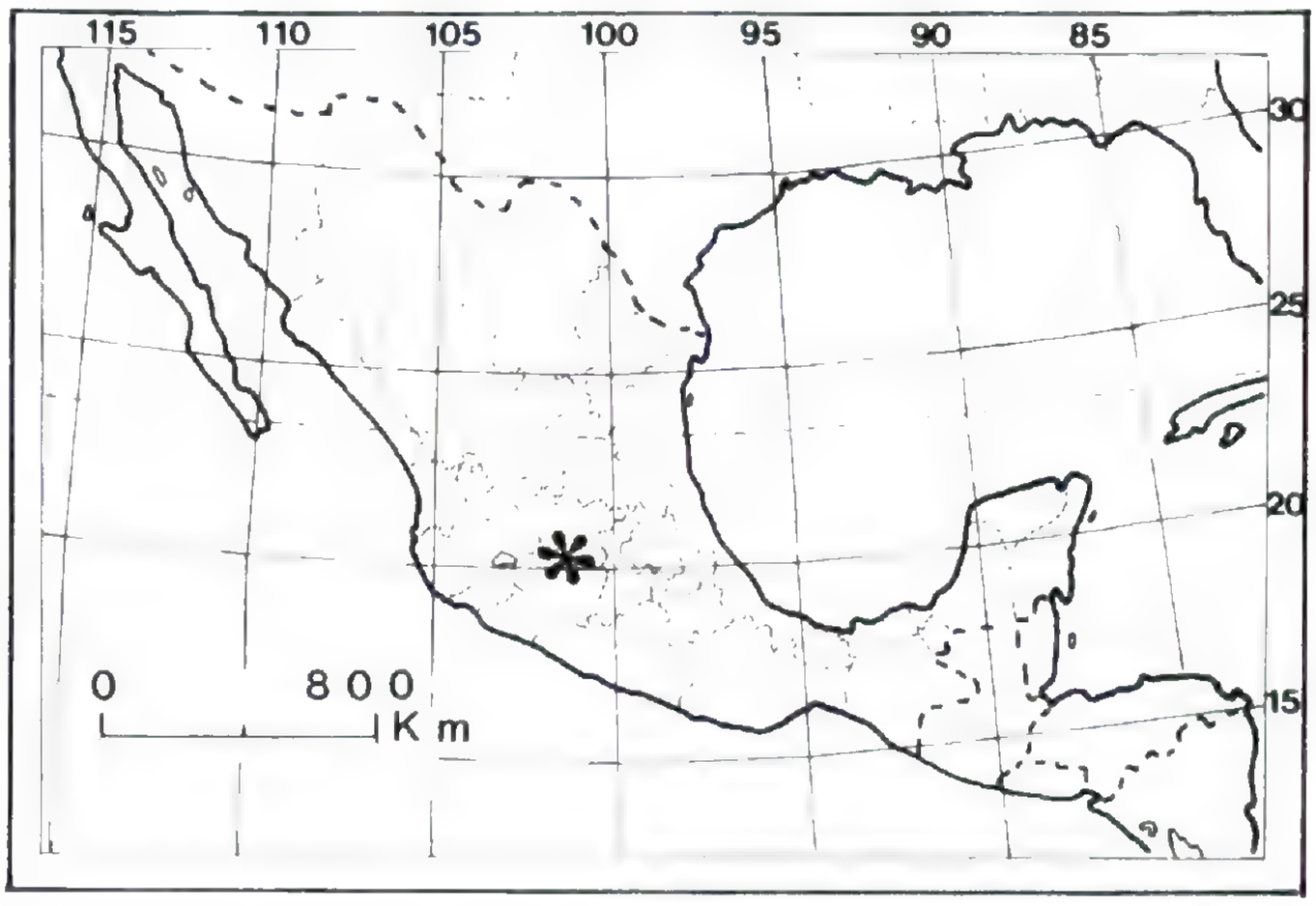
Km
*








A 2 cm

B 1 cm

C-F 4 mm

G-H 2 mm

I-J 1 mm

L-M 0 5 mm

A

H

I

B



C

M

N

O

J

D

E

F

G

K

L

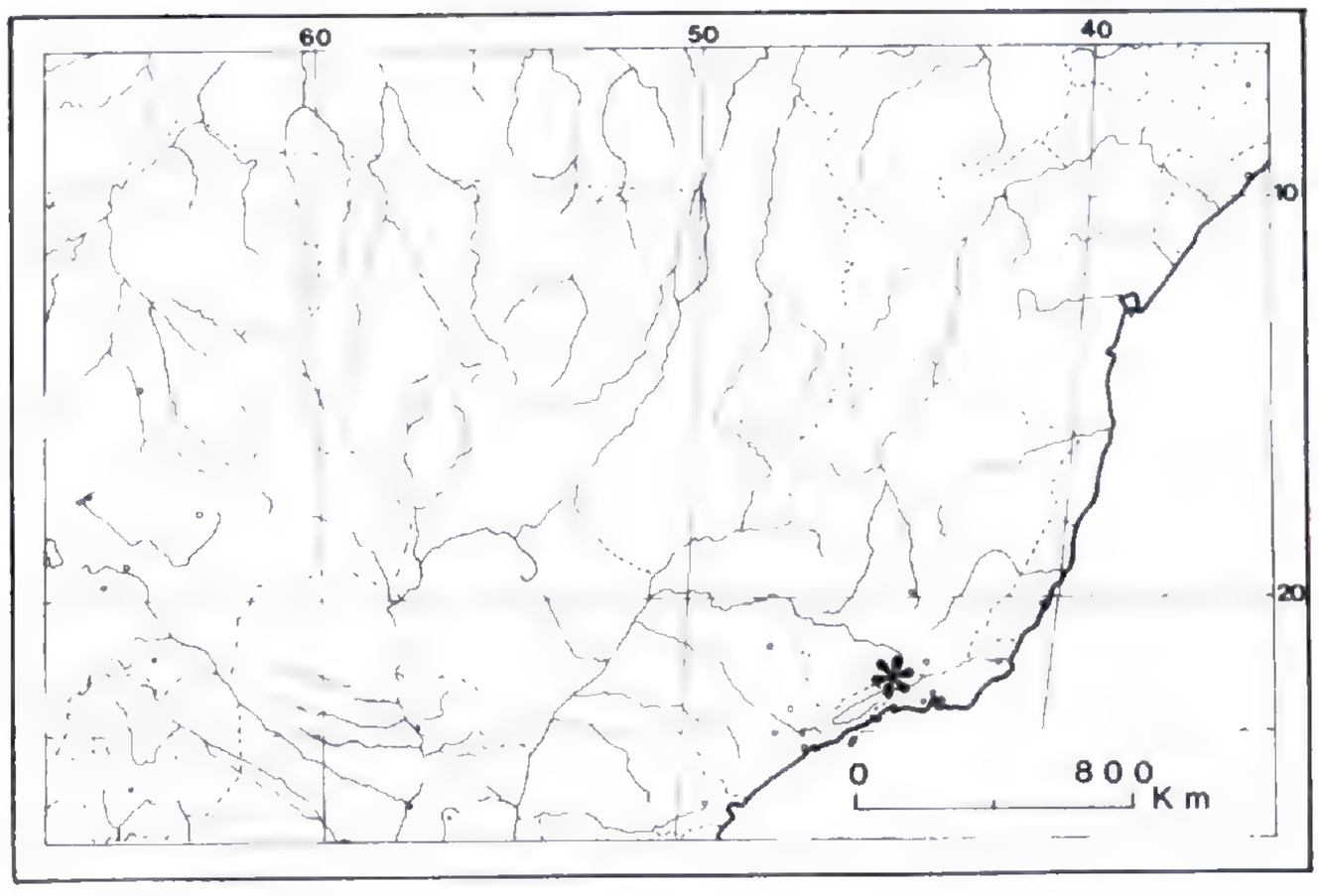
A 3cm

B-C 5mm

D-G 2 mm

H-L 1 mm

M-O 0.5mm



**17. Chionolaena wittigiana** Baker in Martius, Fl. Bras. 6: 129. 1882. TYPE: Brazil. Minas Gerais: in cacumine Serra de Itatiaia, *Glaziou 6590* (lectotype, selected here, K; isolectotype, C). Figure 21.

Woody shrub with ascendent, erect, and densely leafy stems, 15–30 cm high. *Leaves* linear or linear elliptic, stiff, 2–2.5 cm long, 1.5–3 mm wide with slightly revolute margins, adaxially arachnoid pubescent, densely lanate and whitish abaxially. *Capitula* heterogamous, numerous, arranged in dense corymbs, sessile and terminal on the upper branches. *Involucre* obdeltate. Involucral bracts 20–24; outer bracts linear ovate, acuminate, 4–5 mm long, 1 mm wide; inner bracts 5–6 mm long, 0.5–0.8 mm wide. *Florets* 12–24, functionally staminate florets more numerous than pistillate florets. *Pistillate florets* 8–9; corollas 1.8–3 mm long; achenes oblong elliptic, 0.5–0.8 mm long, 0.3–0.4 mm wide, pubescent with long, apically acute, duplex hairs. *Functionally staminate florets* 12–15; corollas 1.5–2.2 mm long; style branches truncate, 0.25–0.30 mm long; anthers 1–1.8 mm long with tails equaling antheropodium; ovaries sterile, flattened or contracted toward middle, 0.4–0.6 mm long, 0.3 mm wide, pubescence as in pistillate florets.

*Distribution.* Restricted to the state of Minas Gerais in southeastern Brazil. This species is found on stony and rocky mountain slopes between 2,400 and 2,600 m. Flowering collections were made in October and November.

*Chionolaena wittigiana* is recognized by its linear, somewhat stiff leaves and the heterogamous capitula arranged in compact corymbs.

*Additional specimens examined.* BRAZIL. MINAS GERAIS: Itatiaia, 9 July 1872, *Glaziou 5896* (paratype of *Chionolaena glomerata*) (P); Serra do Itatiaia, ca. 2,400 m, "in rupibus," 19 Oct. 1903, *Dusén 2132* (S); Itatiaia, Agulhas Negras, 2,600 m, 22–28 Jan. 1938, *Markgraf & Brade 5704* (herb. No. 39366, NY); Agulhas Negras, Serra do Itatiaia, 30 Dec. 1895, *Ule 3733* (HBG).

## DUBIOUS SPECIES

*Chionolaena longifolia* Baker in Martius, Fl. Bras. 6(3): 131. 1882.

I have not found specimens of *C. longifolia* in any herbaria where I have studied. Baker (1882: 131) cited only one collection of *C. longifolia* (*Sellow 2114*). The type was probably destroyed. There is a photograph distributed by the Field Museum of Natural History (No. 15146) as the type for *C. longifolia*. The photograph agrees with Baker's description; however, the label on the photo reads: "*Sello 853*" instead of *Sello 2114*. It therefore must be excluded from the original material.

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## Index of Scientific Names

Synonyms are in *italics*.
New names and combinations are in **boldface**.

*Achyrocline capitata* Baker
*Anaphalis aecidiocephala* Grierson
Chionolaena DC.
aecidiocephala (Grierson) Anderberg & Freire
arbuscula DC.
*arbuscula DC.* var. *hololeuca* Baker ex Glaz.
*breweri* Steyerm.
**capitata** (Baker in Martius) Freire
columbiana S. F. Blake
concinna (A. Gray) Anderberg & Freire
*corymbosa* Hemsley
**chrysocoma** (Wedd.) Freire
eleagnoides Klatt
*glaziovii* Baker
*glomerata* Baker
*innovans* Wawra
isabellae Baker
jeffreyi H. Robinson
latifolia (Benth.) Baker
*lavandulaceum* Benth. & Hook. f. ex Hemsley
lavandulifolia (Kunth) Benth. & Hook. f. ex B. D. Jackson
longifolia Baker
lychnophorioides Sch.-Bip.
**mexicana** Freire
phylicoides (Gardner) Baker
sartorii Klatt
**seemannii** (Sch.-Bip. in Seemann) Freire
wittigiana Baker
*Elichrysum lavandulaefolium* Kunth
*lavandulaefolium* DC.
*Gnaphalium aecidiocephala* (Grierson) L. O. Williams
*concinnum* A. Gray
*eleagnoides* (Klatt) S. F. Blake
*hypochaionaeum* Sch.-Bip. ex Klatt
*lavandulaceum* DC.
*lavandulaefolium* (Kunth) S. F. Blake
*sartorii* Sch.-Bip. ex Klatt
*sartorii* (Klatt) F. J. Espinosa Garcia
*seemannii* Sch.-Bip.
*Leucopholis* Gardner
*capitata* (Baker) Cufod.
*latifolia* Benth.
*phylicoides* Gardner
*Oligandra chrysocoma* Wedd.

## Numerical List of Taxa

*Chionolaena*

(1) *C. aecidiocephala* (Grierson) Anderberg & Freire
(2) *C. arbuscula* DC.
(3) *C. capitata* (Baker in Martius) Freire
(4) *C. columbiana* S. F. Blake
(5) *C. concinna* (A. Gray) Freire
(6) *C. chrysocoma* (Wedd.) Freire
(7) *C. eleagnoides* Klatt
(8) *C. isabellae* Baker
(9) *C. jeffreyi* H. Robinson
(10) *C. latifolia* (Benth.) Baker
(11) *C. lavandulifolia* (Kunth) Benth. & Hook. f. ex B. D. Jackson
(12) *C. lychnophorioides* Sch.-Bip.
(13) *C. mexicana* Freire
(14) *C. phylicoides* (Gardner) Baker
(15) *C. sartorii* Klatt
(16) *C. seemannii* (Sch.-Bip.) Freire
(17) *C. wittigiana* Baker

## List of Exsiccatae

The figures in parentheses refer to the species number. Numbers correspond to those given in the numerical list of taxa.

Balls, B5139 (11). Barclay & Juajibioy, 6927 (4). Beaman, 1961 (11); 2145 (11); 3511 (11). Brade, A. C., 757 (8); 6385 (8); 12659 (3); 12733 (8); 15596 (8); 15597 (10); 15599 (3); 16517 (14); 16898 (3); 17004 (14); 17012 (14); 17013 (3); 17421 (8); 20282 (8); 21260 (8).

Cabrera, A. L., 12227 (14). Cabrera, A. L. & H. Fabris, 14212 (3). Camerik, 29 (8). Campos Porto, 1218 (2). Carriker, 15 (4). Chase, 9389 (12); 9708 (3). Claussen, year 1839 (2). Cuatrecasas & Castañeda, 25115 (4).

Damazio, L., 1159 (2). Dionisio & Octavio, 28 June 1942 (14). Dusén, 395 (10); 468 (3); 542 (8); 2007 (10); 2132 (17); *s.n.* year 19..S870128 (3).

Eiten, G. & L. T. Eiten, 6553 (10). Equipe do Projecto Serra dos Orgãos, 1 Nov. 1970 (14). Farney et al., 800 (14).

Gardner, 5772 (14). Glaziou, 4840 (8); 4841 (10); 4843 (3); 4851 (10); 5896 (17); 5899 (3); 5903 (10); 6590 (17); 6593 (3); 6601 (8); 7723 (3); 8768 (3); 8769 (8); 11036 (2); 14959 (2); 14960 (12); 14960a (12); 14961 (14); 16157 (14). Gounelle, Feb. 1899 (8). Grant, M. L., 10864 (4). Guchioni, 940 (8). Handro, O., 9423 (3).

Harley, R. M., et al., 19677 (9). Hemmendorff, 632 (8); 633 (3); 648 (10). Holm, R. W. & H. H. Iltis, 573 (11). Horn, 38 (11).

Irwin et al., 29023 (2); 29310 (2).

Joly, C. A., et al., 6790 (3).

King, R. M., et al., 8141 (9). Kirkbride, H. & E. Forero, 1803 (4). Krieger & Urbano, 8649 (2). Kupper, 1148 (11); 1301 (11), 1301a (11).

Liebman, 308 (15); 316 (7). Liesner, R. L., 17987 (10). Lindeman & Haas, 4134 (8); 5197 (8). Lua & Nogueira, 30 (3). Luederwaldt, 16733 pro parte (8); 16733 pro parte (10). Luetzelburg, 6252a, b (14); 6386 (14).

MacDougall, 4129 (1), 6 Jan. 1961 (1). Macedo, A., 2801 (12). Magalhaes, 1696 (12). Maguire, B., et al., 65587 (10). Markgraf, 10102 (14). Markgraf & Brade, 3702 (10); 5704 (17). Martii, 829 (2). Martinelli, 7762 (3). Martinelli & Simonis, 9051 (14). Martinelli, G., et al., 10843 (8). Martius, 843 (2). Merxmüller & Sammuel, 25605 (8).

Oakes Ames, 26 Dec. 1915 (8); 26 Dec. 1916 (10). Oersted, 10570 (11).

Pabst, 3473 (2). Parry & Palmer, 423 (5). Pereira, E., 208 (14); 2637 (2). Pittier, 3430 (11). Pringle, 4223 (11); 7700 (13). Purpus, 1523 (11); 2990 (11).

Rangel, O. & A. Cleef, 934 (6). Rangel et al., 988 (4). Rizzini, 5 June 1951 (14); 368 (14). Romero & Castañeda, 7356 (4). Ross, 1265 (11). Roth, P. L., 1401 (2) Rzedowski, 35551 (11).

Schlim, 809 (6). Schaffner, 222 (5). Shenell, 8432 (14). Schuch, *s.n.* "Brasilia" (2). Seemann, 1994 (16). Seifriz, W., 494 (4). Smith, 1682 (10). Steyermark, J. & F. Delascio, 129265 (10). Steyermark, J. & B. Holst, 130822 (10). Steyermark, J., et al., 126074 (10); 126322 (10). Sucre, 5765 (3). Sucre & Krieger, 6836 (12).

Tamandaré, F., 6384 (3). Tamandaré, F. & A. C. Brade, 6383 (3). Troll, 721 (11).

Ule, E., 2601 (12); 2602 (2); 3374 (8); 3733 (17); 3913 (3).

Vauthier, M., 298 (2). Vianna, 197 (8). Voll, O., 2 Jan. 1937 (14).

Wawra, H., 396 (3); 420 (8). Weston, 1551 (11); 5877 (11); 10122 (11).

# A REVISION OF *MALVAVISCUS* (MALVACEAE)[1]

*Billie L. Turner*[2] *and*
*Meghan G. Mendenhall*[3]

## ABSTRACT

Comprehensive reevaluation of herbarium material of the genus *Malvaviscus* yields two widespread species, *M. arboreus* of North America and *M. concinnus* of South America, two localized species, *M. achanioides* of Mexico and *M. williamsii* of Peru and Colombia, and a widespread cultivar of unknown origin, *M. penduliflorus*.

In spite of recent attempts to delimit and classify its many specific and subspecific taxa, *Malvaviscus* (Malvaceae) remains enigmatic. The genus is highly variable morphologically and given to populational forms. Furthermore, these forms intergrade producing an array of character combinations. An extreme taxonomic treatment of the genus would recognize a horde of intergrading forms. Indeed, this extreme infrageneric variation has led to the proposal of over 50 specific names within *Malvaviscus*, though Schery (1942) recognized only three in his monograph of the genus.

Because of the common intergradation and recombination of character states, few characters within *Malvaviscus* have proven useful for specific recognition. Modern interpretations of the genus have generally recognized about a dozen overlapping taxa. However, we believe that the overwhelming majority of the species proposed under *Malvaviscus* represent only two biologically significant taxa, *M. arboreus* in North America and *M. concinnus* in South America.

## HISTORY OF THE GENUS

The genus *Malvaviscus* was established almost 200 years prior to its monograph by Schery (1942). Among the first generic names to include *Malvaviscus* were *Alcea*, *Althaea*, and *Malva*. Linnaeus did not recognize the genus and placed its species in *Hibiscus* in 1753. In 1759, Fabricius distinguished *Malvaviscus* based on a single species, i.e., *Hibiscus malvaviscus* L. (A discussion of the typification of *Malvaviscus* can be found in Taxon 17: 87, 1968.) In 1788, Swartz proposed to rename the genus as *Achania*. In 1824, A. P. de Candolle divided *Malvaviscus* into two sections: *Achania* and *Anotea*. *Anotea* was raised to generic rank by Kunth in 1846, and *Achania* is now recognized as synonymous with *Malvaviscus*.

Generic treatments have not been in agreement. Schery's monograph (1942) included a complex of 11 varieties of *M. arboreus* as well as two additional species that have since been transferred to *Pavonia*. Other treatments, which have recognized up to a dozen species, occur in floras throughout the range of *Malvaviscus* (Robyns, 1966; Standley, 1923; Standley & Steyermark, 1949). However, the only significant treatment of the genus since Schery has been the exemplary work of Fryxell (1988) in his monograph of the Malvaceae of Mexico. In his discussion of the taxonomic problems within *Malvaviscus*, Fryxell acknowledged the difficulty of clearly delimiting species: "There is a certain sameness of morphology that runs through the genus, and clear-cut differentiating characters are lacking." Fryxell recognized six species of *Malvaviscus* in Mexico, three of which are maintained here.

## CHROMOSOME NUMBERS

The first report of a chromosome count for *Malvaviscus* was presented by Skovsted in 1935 (Table 1). He reported a count of $2n$ = ca. 84 for an unidentified cultivated species in Kew Gardens, presumably obtained originally "from gardens on the Gold Coast." We take the species to be *M. penduliflorus* of the present treatment since Skovsted noted:

> Morphologically, the type under observation is distinctly different from the wild growing *M. arboreus* Cav. Its

[1] We are grateful for the encouragement and helpful comments of our esteemed colleague, Paul Fryxell, throughout the course of this study. Our investigation is based upon the examination of approximately 3,200 specimens on deposit at the following institutions: BRG (3), F (701), herb. Fryxell (2), GH (431), HUA (7), LL (200), MG (6), MO (783), NY (492), RB (6), SP (9), TEX (170), US (381). Nancy Webber provided the illustration.

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TABLE 1. Chromosome numbers in *Malvaviscus*.

| Taxon | 2*n* number | Voucher/reference |
|---|---|---|
| *M. arboreus* var. *arboreus* reported as var. *mexicanus* | ca. 56 | Mexico. Veracruz: *Fryxell & Bates 940*; Bates (1976) |
| *M. arboreus* var. *arboreus* reported as var. *mexicanus* | ca. 56 | Mexico. Veracruz: *Fryxell et al. 1676*; Bates (1976) |
| *M. arboreus* var. *arboreus* reported as *M. penduliflorus* | ca. 28 | Mexico. Jalisco: *Fryxell, Bates & Blanchard 1575*; Bates (1976) |
| *M. arboreus* var. *drummondii* | ca. 28 | U.S.A. Texas: Travis Co., *Mendenhall 485*; reported here |
| *M. penduliflorus* reported as *M.* sp. | ca. 84 | Kew Gardens, where cultivated; Skovsted (1935) |
| *M. penduliflorus* | 86 | India. Karnataka: where cultivated; Krishnappa & Munirajappa (1982) |

cytological behaviour indicates that it is probably a hybrid although its origin appears unknown. It is commonly cultivated in Trinidad where it is vegetatively reproduced as it is apparently completely sterile.

Krishnappa & Munirajappa (1982), however, reported *M. penduliflorus* to have a count of $2n = 86$, presumably a miscount of $2n = 84$, or possibly an aneuploid clonal derivative of what would seem to be its original number, $2n = 84$, since other taxa in *Malvaviscus* appear to have an ancestral base number of $x = 14$, if not $x = 7$. Bates (1976) listed a count of $2n =$ ca. 28 for *M. penduliflorus*, but we believe the voucher concerned is more likely a morphological variant of the widespread, highly variable *M. arboreus* var. *arboreus*, as conceived of here.

Our report of $2n =$ ca. 14 pairs for *M. arboreus* var. *drummondii* is to some extent biased because of the report of $2n = 28$ by previous workers. In truth, the count would have been any number between 12 and 15 pairs, the chromosomes being very small and not forming neat bivalents.

In summary, only two taxa of *Malvaviscus* have been counted with reasonable certainty to date: *M. arboreus* var. *arboreus* with $2n =$ ca. 28 and ca. 56, and the cultivated *M. penduliflorus* with counts of $2n =$ ca. 84 and 86 (Table 1). The base number of the genus appears to be $x = 14$, if not 7. The latter base would agree with that found in the large, closely related genus *Pavonia*, where some 35 or more species have been counted, all on a base of $x = 7$, ranging from $n = 14$ to $n = 56$ (although some authors have reported occasional counts of both $n = 13$ for a species that otherwise has been counted as $n = 14$ (e.g., *Pavonia zeylanica* (L.) Cav. with $2n = 52$ (Krishnappa & Munirajappa, 1980) vs. $2n = 56$ (Dasgupta & Bhatt, 1976, 1981, 1982)).

## SPECIES CONCEPT

In this treatment, species concepts in *Malvaviscus* are largely those of the senior author, the junior author being new at the herbarium bench. Because fieldwork on the genus was limited, species concepts are based on morphogeographical considerations and our experience with species recognition in other groups (e.g., Asteraceae, Fabaceae), both in the field and as hypothesized by herbarium evaluations. We believe our specific delimitations in *Malvaviscus* are populational in nature and are comparable to what most workers refer to as good species. We do not claim this to be true for *M. penduliflorus*, for we suspect that the plants referable to this species are relatively uniform, mostly sterile cultivars, developed very early on by accidental or synthetic means. We have recognized *M. penduliflorus* as a "synthetic species," not occurring naturally in the wild except as it has persisted or escaped cultivation by vegetative means, although it is possible that occasional hybrids between *M. penduliflorus* and *M. arboreus* might occur, as noted under the discussion that follows each.

Our species concepts are similar to those of previous revisional workers on *Malvaviscus*, namely Schery (1942) and Fryxell (1988). In spite of the plethora of pressed specimens available for study, extraordinary variation, and widespread distribution of *Malvaviscus*, Schery recognized a single species with eleven varieties while Fryxell recognized six species in Mexico, which suggests that he would likely have recognized less than ten taxa for the remainder of its distribution. In short, our recognition of five species for *Malvaviscus* (including *M. penduliflorus*) is conservative, standing between the evaluations rendered by Schery and Fryxell. Except for *M. penduliflorus*, we believe

the taxa that we have recognized are comparable in nature and constitute populational or biological units that can be verified by future field workers.

## Taxonomic Treatment

**Malvaviscus** Fabr., Enum. 155. 1759. TYPE: *Hibiscus malvaviscus* L. [= *Malvaviscus arboreus* Cav.]. See Dandy (1966) for typification of *Malvaviscus*.

*Achania* Sw., Prodr. 102. 1788. TYPE: *Achania pilosa* Sw.

Erect or clambering (vinelike) shrubs or small trees, pubescent or glabrous. Leaves petiolate, the blades linear-lanceolate to broadly ovate-cordate, unlobed to 3–5-lobed, serrate to subentire; stipules subulate, deciduous. Flowers solitary or several in the leaf axils or sometimes in apical cymes; bractlets of the involucel linear to obovate (rarely broadly ovate), usually (5–)8–9; calyx campanulate or tubular, 5-lobed; petals 5, red (rarely white), asymmetrically obovate-cuneate, auriculate toward the base, forming a tubular corolla; androecium usually exserted, the staminal column with 5 apical teeth, the filaments short and ± retrorse; styles 10 with capitate stigmas. Fruit a fleshy schizocarp, oblate, red (rarely white), with 5 carpels, each 1-seeded. Base chromosome number, $x = 14$.

*Diagnosis and relationships.* *Malvaviscus* is a member of the tribe Malvavisceae C. Presl, Reliq. Haenk. 2: 135, 1835 (as "Malvaviscaceae") by virtue of its five uniovulate carpels, schizocarpic fruit, ten free styles, and apically 5-toothed staminal column. Distinguishing generic characters of *Malvaviscus* are its auriculate petal and red or rarely white baccate fruit. The petal auricle is the basal lobe that gives each petal its characteristic mitten shape. Apical lobes are called simply lobes. The genera thought to be closest to *Malvaviscus* are *Pavonia*, *Lopimia*, and *Anotea*. The largest of these, *Pavonia*, has dry fruits. *Lopimia* and *Anotea* are small genera that have blue-black fruits (dry in *Lopimia*) and lack the auriculate petal.

Although *Malvaviscus* can be found in gardens throughout the tropical and subtropical world, it is native to the Western Hemisphere. Its range extends from Peru and northern Brazil to the southern United States and the West Indies. Although individuals and populations are highly variable, especially in Mexico and Central America, we recognize two major taxa, *M. arboreus* in the north and *M. concinnus* in the south. A third, relatively localized species of northwesternmost South America, *M. williamsii*, is recognized but clearly belongs to the *M. concinnus* complex. Were the characters that mark it not so easily identified, and if it had not already been treated at the specific level, we would probably have recognized this as an intergrading variety of the latter. Finally, for practicality, we maintain two species that would otherwise be absorbed by *M. arboreus*. These are *M. penduliflorus*, a distinctive hybrid cultivar, and *M. achanioides*, an intermediate form between *M. arboreus* and *M. concinnus*.

## Key to Species of *Malvaviscus*

1a. Leaves mostly 15–35 cm long, the blades usually strongly cordate; vestiture of peduncles mostly pilose; corollas mostly 40–70 mm long; calyces mostly 18–30 mm long; fruits mostly 15–30 mm across; South America, Panama, Costa Rica, and Gulf slopes of Honduras and Mexico (Chiapas, Tabasco, Veracruz).
  2a. Calyces mostly 18–20 mm long; vestiture of peduncles and petioles densely pilose with hairs 1–3 mm long; Honduras and Mexico ..... 3. *M. achanioides*
  2b. Calyces mostly 20–30 mm long; vestiture of velutinous hairs mostly 0.2–1.5 mm long; South America, Panama, and Costa Rica.
    3a. Involucellar bracts broadly elliptical-ovate, widest at or near the middle, the margins strongly imbricate; Peru and Colombia ..... 5. *M. williamsii*
    3b. Involucellar bracts filiform to linear lanceolate, broadest at or near the base; South America, Panama, and Costa Rica ..... 4. *M. concinnus*

1b. Leaves mostly 5–20 cm long, if longer the blades ovate to elliptical, abruptly to not at all cordate; vestiture various but not usually densely pilose with hairs 1–3 mm long; corollas mostly 15–70 mm long; calyces mostly 8–18(–20) mm long; fruits, when present, mostly 8–14 mm across; North America and West Indies or else cultivated.
  4a. Cultivated, mostly sterile, rarely producing fruits; flowers pendulous, the corollas mostly 42–70 mm long; leaves ovate and subglabrous; widespread in gardens, and often escaping or persisting following cultivation ..... 2. *M. penduliflorus*
  4b. Wild and cultivated, usually fertile and producing red or white fruits; flowers usually erect, the corollas mostly 15–50 mm long; leaves variable in shape and vestiture; throughout southern and central Mexico, southeastern United States, West Indies, and rarely coastal areas of northern South America, occasionally cultivated and persisting elsewhere.
    5a. Leaves rather uniformly 3-lobed and mostly obtuse at the apex, strongly cordate; stems and petioles diffusely pubescent with overlapping stellate hairs that form a velvety vestiture only rarely exceeding 0.25 mm high;

mostly United States, just barely extending into Mexico along the Gulf coastal regions of Tamaulipas ..... 1b. *M. arboreus* var. *drummondii*

5b. Leaves various, but the blades usually acute at the apices, truncate or cordate; stem and petioles variously pubescent to glabrous, but the vestiture usually not as described above, if evenly velvety-pubescent then some or most of the hairs exceeding 0.25 mm; widespread throughout tropical and subtropical habitats of Mexico, Central America, and West Indies, rarely elsewhere in cultivation ..... 1a. *M. arboreus* var. *arboreus*

**1. Malvaviscus arboreus** Cav., Diss. 3: 131. t. 48. 1787.

**1a. Malvaviscus arboreus** var. **arboreus**

**Malvaviscus arboreus** Cav., Diss. 3: 131. t. 48. f. 1. 1787. *Hibiscus malvaviscus* L., Sp. Pl. 694. 1753. *Malvaviscus coccineus* Medikus, Malvenfam. 49. 1787, nom. superfl. *Achania malvaviscus* (L.) Sw., Prodr. 102. 1788. *Achania coccinea* Salisb. Prodr. 385. 1796, nom. superfl. *Malvaviscus malvaviscus* (L.) Millsp., Publ. Field Columbian Mus., Bot. Ser. 2: 73. 1900. TYPE: "Hibiscus malvaviscus" (holotype, LINN-875.22).

*Achania mollis* Aiton, Hort Kew. 2: 459. 1789. *Malvaviscus mollis* (Aiton) DC., Prodr. 1: 445. 1824. TYPE: Mexico (holotype, BM not seen, without additional information according to Fryxell, 1988).

*Achania pilosa* Sw., Prodr. 102. 1788. *Malvaviscus pilosus* (Sw.) DC., Prodr. 1: 445. 1824. *Hibiscus pilosus* (Sw.) Fawcett & Rendle, Fl. Jamaica 5: 137. 1926. TYPE: Jamaica. *Swartz s.n.* (holotype, S not seen, according to Fryxell, 1988).

*Pavonia spiralis* Cav., Icon. 5: 20. t. 434. 1799. *Malvaviscus ciliatus* DC., Prodr. 1: 445. 1824, nom. superfl. *Achania ciliata* Sprengel, Syst. Veg. 3: 100. 1826, nom. superfl. TYPE: Panama. Taboga Island, *Née s.n.* (holotype, MA not seen).

*Malvaviscus cordifolius* Moench, Meth. Suppl. 208. 1802. TYPE: no longer extant, according to Stafleu & Cowan (1981).

*Malvaviscus acapulcensis* Kunth, Nov. Gen. Sp. 5: 288 [folio ed. p. 224]. 1822. TYPE: Mexico. Guerrero: near Acapulco, *Humboldt & Bonpland*, 1803 (holotype, P-HBK not seen, according to Fryxell, 1988).

*Malvaviscus grandiflorus* Kunth, Nov. Gen. Sp. 5: 286 [folio ed. p. 223]. 1822. TYPE: Mexico. Guanajuato: prope Guanajuato, *Humboldt & Bonpland*, 1803 (holotype, P-HBK not seen; fragment holotype, F).

*Malvaviscus pentacarpus* DC., Prodr. 1: 445. 1824. TYPE: Icones Florae Mexicanae no. 124 (Torner Collection acc. no. 631.1093, Hunt Institute). (Cf. photo F-30507 of G copy (not the type), according to Fryxell, 1988.)

*Malvaviscus arboreus* var. *cubensis* Schldl., Linnaea 11: 360. 1837. *Malvaviscus arboreus* subsp. *cubensis* (Schldl.) Hadač, Folia Geobot. Phytotax. Praha 5: 432. 1970. TYPE: Cuba. *Poeppig s.n.* ex herb. Kunze (holotype, LZ destroyed; isotype, W? not seen, according to Fryxell, 1988).

*Pavonia urticaefolia* C. Presl, Reliq. Haenk. 2: 128. 1835. *Malvaviscus urticifolius* (C. Presl) Fryxell, Syst. Bot. 12: 279. 1987. TYPE: Mexico. "In terris occidentalibus" (probably in the state of Guerrero or Mexico during Haenke's trip from Acapulco to Mexico City and return during Nov.–Dec. 1791), *Haenke s.n.* (lectotype, designated by Fryxell (1988), PR-197902A not seen; isolectotype, PR-197902B not seen).

*Malvaviscus sepium* Schldl., Linnaea 11: 361. 1837. *Malvaviscus arboreus* var. *sepium* (Schldl.) Schery, Ann. Missouri Bot. Gard. 29: 226. 1942. TYPE: Mexico. Veracruz: near Xalapa, June 1829, *Schiede 480* (holotype, B destroyed; photoholotype, F, NY).

*Malvaviscus arboreus* var. *mexicanus* Schldl., Linnaea 11: 359. 1837. TYPE: Mexico. Veracruz: near Veracruz, *Schiede s.n.* (lectotype, designated by Fryxell (1988), HAL not seen).

*Malvaviscus brevipes* Benth., Bot. Voy. Sulphur 68. 1844. TYPE: Costa Rica. Nicoya, *Barclay s.n.* (holotype, BM not seen, according to Fryxell, 1988).

*Malvaviscus sagraeanus* A. Rich., Hist. Phys. Cuba, Pl. Vasc. 131. t. 14. 1845 [1841]. *Malvaviscus arboreus* var. *sagraeanus* (A. Rich.) E. G. Baker, J. Bot. 37: 345. 1899. TYPE: Cuba, *de la Sagra s.n.* (holotype, P? not seen; isotype, K not seen, according to Fryxell, 1988).

*Malvaviscus pulvinatus* A. Rich., Hist. Phys. Cuba, Pl. Vasc. 133. 1845 [1841]. TYPE: Cuba, *de la Sagra s.n.* (specimen unknown, according to Fryxell, 1988).

*Malvaviscus arboreus* var. *parviflorus* Griseb., Fl. Brit. W. I. 83. 1859. TYPE: Jamaica. Without locality, without date, *Wullschlaegel 768* (holotype, GOET not seen, according to Fryxell, 1988).

*Malvaviscus palmanus* Pittier & J. D. Smith, Bot. Gaz. (Crawfordsville) 23: 238. 1897. *Malvaviscus arboreus* var. *palmanus* (Pittier & J. D. Smith) Schery, Ann. Missouri Bot. Gard. 29: 222. 1942. TYPE: Costa Rica. San José: forests of La Palma, 5,100 ft., July 1895, *Tonduz 9712* (holotype, CR not seen; isotype, US; photoisotype, MO).

*Malvaviscus arboreus* var. *sloanei* E. G. Baker, J. Bot. 37: 345. 1899. TYPE: Jamaica. Sloane's Herb. vol. iv. F. 45 (holotype, BM not seen, according to Fryxell, 1988).

*Malvaviscus brevibracteatus* E. G. Baker, J. Bot. 37: 347. 1899. TYPE: Belize. Stann Creek, 27 Dec. 1899, *J. Robertson 34, 35* (syntypes, BM not seen, according to Fryxell, 1988).

*Malvaviscus lanceolatus* Rose, Contr. U.S. Natl. Herb. 5: 175. 1899. TYPE: Mexico. Chiapas: near Cicharras, 12–15 Feb. 1896, *Nelson 3807* (holotype, US; isotypes, GH—2 sheets).

*Malvaviscus arboreus* var. *grisebachii* E. G. Baker, J. Bot. 37: 345. 1899. TYPE: Jamaica. (Based on *M. arboreus* var. α Grisebach, which apparently applies to a vestiture form of *M. arboreus* var. *arboreus*.) Grisebach cited no specimen; neither did Baker. Any lectotype, if designation is needed, would presumably reside at BM or K.

*Malvaviscus polakowskii* E. G. Baker, J. Bot. 37: 346. 1899. TYPE: Costa Rica. Without specific locality,

without date, *Polakowsky 197* (holotype, BM not seen).

*Malvaviscus jordan-mottii* Millsp., Publ. Field Columbian Mus., Bot. Ser. 2: 73. 1900. TYPE: Cayman Islands. Cayman Brac, above Spot Bay, 8 Feb. 1899, *Millspaugh 1166* (holotype, F).

*Malvaviscus rivularis* Brandegee, Zoe 5: 211. 1905. TYPE: Mexico. Sinaloa: near Culiacán, banks of the Cofradia River, *Brandegee*, 1904 (holotype, UC not seen; isotype, US).

*Malvaviscus conzattii* Greenman, Field Mus. Nat. Hist. Bot. Ser. 2: 333. 1912. TYPE: Mexico. Oaxaca: San Pablo, Huitzo, 1,600 m, 25 Aug. 1907, *Conzatti 1981* (holotype, F; isotype, K not seen).

*Malvaviscus oaxacanus* Standley, Contr. U.S. Natl. Herb. 23: 775. 1923. TYPE: Mexico. Oaxaca: N of Tuxtepec, 9 Apr. 1894, *Nelson 348* (holotype, US).

*Malvaviscus hintonii* Bullock, Kew Bull. 1937: 291. 1937. *Malvaviscus arboreus* var. *hintonii* (Bullock) Schery, Ann. Missouri Bot. Gard. 29: 217. 1942. TYPE: Mexico. Mexico State: Distr. Temascaltepec, Tejupilco, 15 May 1933, *Hinton 3928* (holotype, K not seen; isotypes, A, NY).

*Malvaviscus arboreus* var. *brihondus* Schery, Ann. Missouri Bot. Gard. 29: 213. 1942. TYPE: Belize. Honey Camp, Sep. 1929, *Lundell 480* (holotype, MO; isotypes, F, US).

*Malvaviscus arboreus* var. *lobatus* Robyns, Ann. Missouri Bot. Gard. 52: 572. 1966. TYPE: Panama. Chiriquí: Fred Collins' Finca at edge of coffee plantation, 6,000 ft., 2 Aug. 1960, *J. Ebinger 692* (holotype, MO; isotype, F).

Erect or clambering shrubs 1–10 m high. Stems variously stellate-pubescent to glabrate, rarely glabrous. Leaves mostly 5–25 cm long, 3–12 cm wide, petioles mostly 1–12 cm long, the blades variously ovate to cordate, less often elliptical, mostly unlobed, but occasionally with shallow subterminal lobes, variously irregularly serrate, or rarely entire, pubescent with mostly stellate hairs, often densely so, but sometimes glabrous or nearly so. Calyces mostly 8–15(–18) mm long, variously pubescent, the hairs simple or stellate, rarely glabrous, the subtending bracts mostly 5–8(–11), linear to linear-oblanceolate. Corollas red, rarely white, mostly (15–)20–42(–50) mm long, the petals mostly imbricate at anthesis, not normally flaring. Staminal column usually exserted for ca. ¼ of its length, rarely included. Fruit usually bright red but sometimes white, 8–14(–16) mm across. Chromosome number, $2n$ = ca. 14 and 28 pairs.

We interpret this widespread, highly variable species as having a single populationally meaningful variety, variety *drummondii*, as noted below. We include in variety *arboreus* most other material previously placed in *M. arboreus* from North America north of Panama, and that from the West Indies. This includes *Malvaviscus arboreus* var. *mexicanus*, recognized by Fryxell (1988), and other taxa accepted by him as distinct, as noted in the synonymy above. *Malvaviscus arboreus* var. *arboreus* is perhaps the most variable species that the senior author has had the displeasure to work with. Detailed mapping of character states in Mexico and other regions reveals a hodge-podge of variation that must relate to localized genetic partitioning, as well as environmental influences. Thus, while any given population is relatively uniform with respect to, say, vestiture or leaf shape, closely contiguous as well as distant populations may show markedly different vestiture types and leaf shapes. The same may be said with respect to corolla and calyx size, and their vestiture.

A similar type of variation to that mentioned above is found throughout the West Indies and in Central America; all of this must be evident from the considerable synonymy and varietal names that have been proposed for *M. arboreus*.

We also believe that at least some of the variation found in *M. arboreus* must have arisen relatively recently by local hybridization with *M. penduliflorus*, a cultivar which, for convenience and because of its wide introduction in gardens throughout the world, we have treated as a species. Evidence for this is mostly speculative (based largely on herbarium collections from areas where *M. arboreus* grows with or near *M. penduliflorus*) for, as noted by Fryxell (1988), *M. penduliflorus* appears to be largely sterile (at least it does not readily set fruit). Nevertheless, occasional plants do develop fruits; indeed, in parts of southern Mexico and Central America, fruiting specimens assignable to that species seem to occur. The latter plants might be viewed as ancestral fruiting stocks of *M. arboreus* (we have treated these as such), from which the remarkably uniform *M. penduliflorus* developed. This is discussed in more detail under the latter.

*Distribution (Figs. 1, 2).* Mexico, West Indies, and throughout most of Central America (occasionally cultivated elsewhere, as indicated below), 0–2,000 m; flowering all seasons.

*Diagnosis and relationships.* We include *M. hintonii* in synonymy under *M. arboreus* var. *arboreus*, although Fryxell (1988) maintained the species (as *M. urticifolius*), while Schery reduced it to varietal rank under *M. arboreus*. The name is applied to specimens with white corollas, which otherwise appear to have the characters of *M. arboreus*. Indeed, it might reside within our concept of *M. penduliflorus*, except for its shorter corollas and pilose vestiture along the upper stems. One of the syntypes of *M. hintonii* (*Hinton 7912*, NY, US) has a notation by the collector that "the

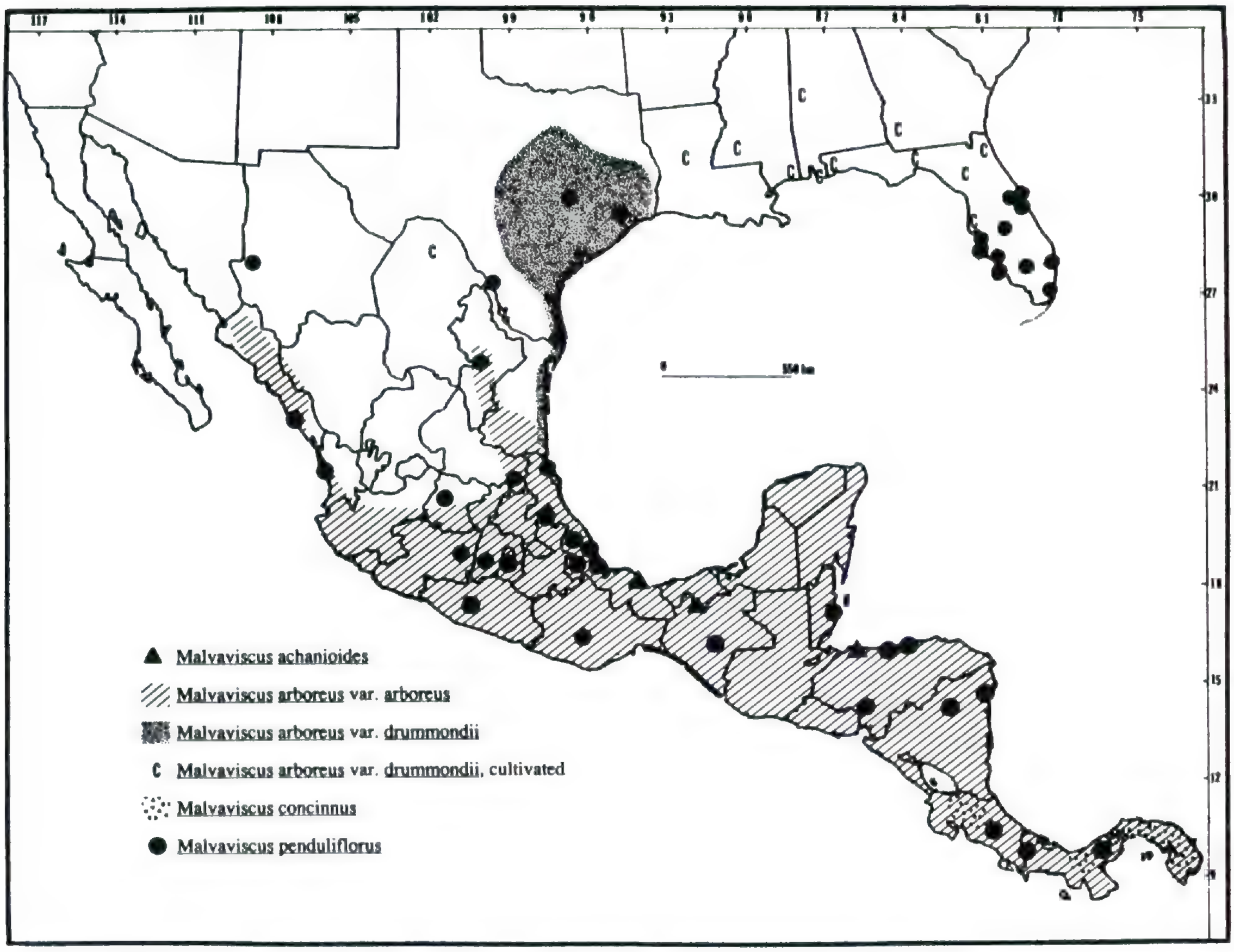


FIGURE 1. Natural distribution of *Malvaviscus* in North and Central America. Isolated collections of *Malvaviscus arboreus* var. *drummondii*, which are marked with "C," are known to be cultivated, thought to have persisted after cultivation, or thought to have escaped from cultivation.

fruit is very rare," suggesting that this might be a color form of *M. penduliflorus*, or perhaps a hybrid segregate between the latter and *M. arboreus*. For additional discussion of this problem see *M. penduliflorus*.

*Malvaviscus conzattii*, because of its relatively large corollas and lanceolate leaves, was relegated to synonymy under *M. penduliflorus* by Schery (1942). Corolla size would position it in our concept of the latter, but its leaf blade shape (having cordate bases) suggests that it belongs to the *M. arboreus* complex, although it is possible that the type concerned is of hybrid origin, as noted above.

*Malvaviscus oaxacanus* and *M. lanceolatus* were both retained by Fryxell (1988), but we believe these to be localized populational "calyx-forms" or "leaf-forms" of *M. arboreus* var. *arboreus*. *Malvaviscus oaxacanus* possesses a rather dense, short, furfuraceous vestiture on the calyces, otherwise it is very similar to *M. arboreus*. *Malvaviscus lanceolatus* has lanceolate-elliptic, nearly glabrous leaves (similar to those of *M. penduliflorus*) and nearly glabrous involucels, otherwise it is very similar to typical *M. arboreus*. Schery (1942) also included both of these names in synonymy under *M. arboreus*.

In an initial "run-through" of the entire *M. arboreus* complex, we thought it possible to recognize *M. lanceolatus* as distinct, but restricted the name to those individuals and/or populations with strictly ovate-elliptic, nearly glabrous leaves and glabrous or nearly glabrous calyces. So construed, the "species" would have comprised (along with the type) the following specimens: MEXICO. CHIAPAS: Mpio. Unión Juárez, between Unión Juárez and Santo Domingo, 1,060 m, 6 Sep. 1980, *Fryxell 3203* (MO, NY). OAXACA. ca. 8.4 mi. S of Putla de Guerrero, ca. 1,000 m, 16 Jan. 1979, *Croat 45810* (MO); Putla, Vicente, ca. 1,200 m, *MacDougall*, 1970 (NY); Juquila, Lachao, Santa Rosa, ca. 1,200 m, *MacDougall*, 1971 (NY); Yaveo, Arroyo San Pedro, 440 m, 23 Mar. 1938, *Mexia 9204* (GH, MO, NY, US); S slope of Sierra S of Lachao, 1,700 m, 5 Dec. 1962, *Moran 10114* (US). Fryxell (1988), however, cited specimens from Nayarit, Jalisco, Morelos, and Puebla that we intended to include within our concept of *M. arboreus* var. *arboreus*, most of these having ovate

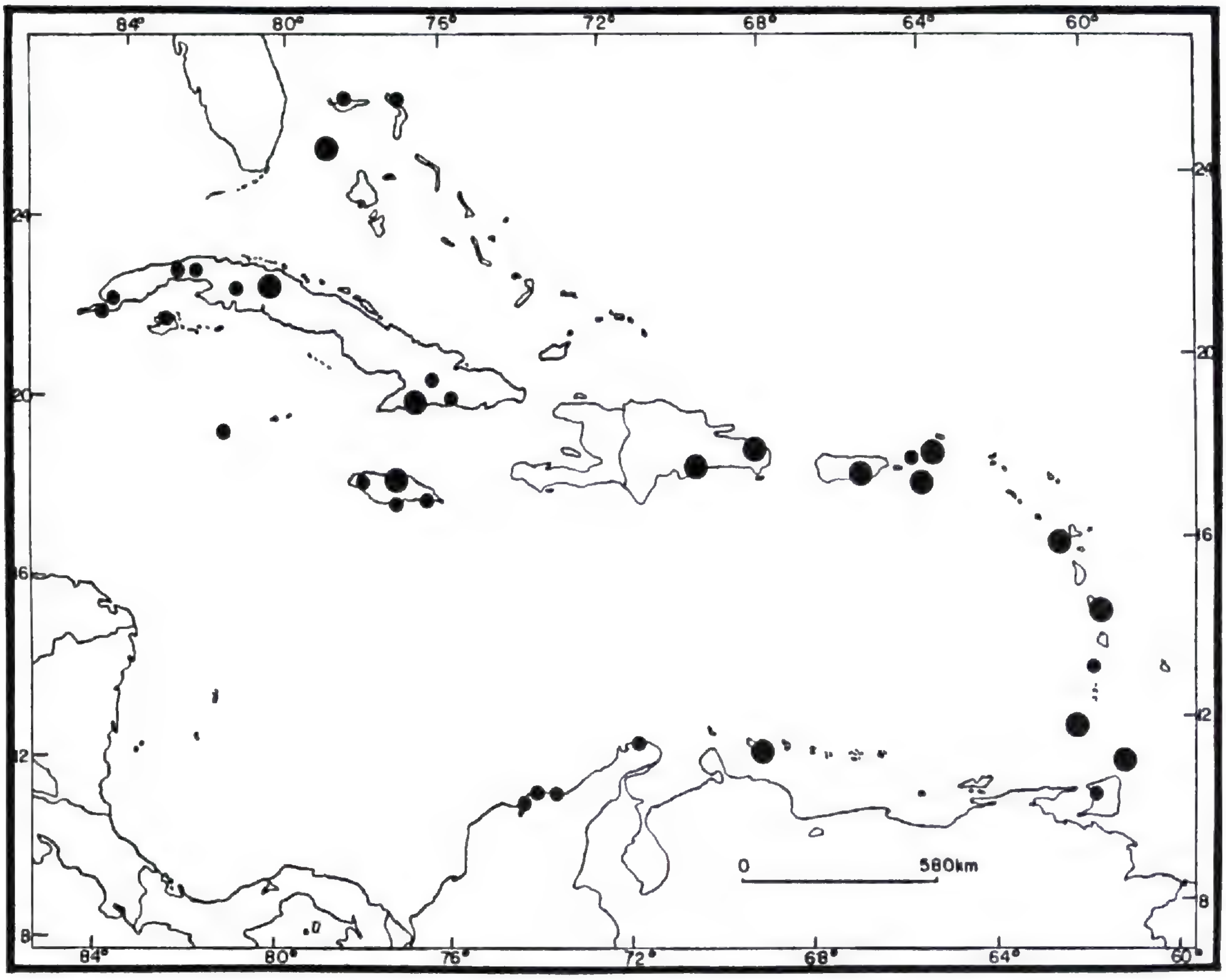


FIGURE 2. Collections of *Malvaviscus arboreus* var. *arboreus* (small closed circles); and *M. penduliflorus* (large closed circles) from the West Indies.

leaf blades and a vestiture reminiscent of the latter. Indeed, all of *M. lanceolatus*, sensu Fryxell, can be submerged within *M. arboreus* without creating much of a morphological ripple, for even as we intended to circumscribe *M. lanceolatus*, the taxon would have differed from *M. arboreus* by a combination of weakly differentiating characters, mainly leaf shape (lanceolate-elliptic), essentially glabrous stems and foliage, relatively large glabrous calyces, and longer corollas (mostly 40–50 mm). The same can be said with respect to the "cultivar," *M. penduliflorus*, for it appears to be a largely sterile derivative from the *M. arboreus* complex centering about *M. lanceolatus* (sensu Fryxell). Indeed, all of the characters that purportedly distinguish *M. penduliflorus* and *M. lanceolatus* from *M. arboreus* crop up in one or more combinations throughout the range of *M. arboreus*, as treated here. For example, *M. palmanus* has been applied to populations from Central America having ovate-elliptic blades and other characters resembling those of *M. lanceolatus*.

In eastern Panama and parts of Costa Rica, *M. arboreus* shows variation in the direction of *M. concinnus*, especially in the size of calyx and fruit and in leaf shape and vestiture, and occasional specimens from this region have been somewhat arbitrarily positioned in one or the other species. A case might be made for the treatment of the mostly South American *M. concinnus* as a broad regional variety of *M. arboreus*, such as was done by Schery (1942) under the name *Malvaviscus arboreus* var. *longifolius*. Strangely, Robyns (1966), in his treatment of *Malvaviscus* for Panama, mentioned none of this variation, relegating all of the Panamanian material that he examined to *M. arboreus* var. *mexicanus*, including the cultivated *M. penduliflorus*. Nevertheless, he described a new variety, *M. arboreus* var. *lobatus*, which is no more than a form of his *M. arboreus* var. *mexicanus* with apically lobed petals.

*Representative specimens examined.* UNITED STATES. FLORIDA: Monroe Co., Big Pine Key, hammock borders, 26 July 1981, *Brumbach 9708* (GH, MO, cultivated?). HAWAII: Maui, Kohala, persistent along roadside, 8 Aug. 1926, *Degener 9840* (NY, cultivated?). LOUISIANA. Orleans Parish, New Orleans, 1 Nov. 1971, *Ewan 23082* (NY, cultivated). NORTH CAROLINA: New

Hanover Co., Wilmington, along railroad cut, 3 Sep. 1970, *Leonard 3714* (GH, NY). MEXICO. CAMPECHE: Tuxpeña, 22 Nov. 1931, *Lundell 970* (A, F, MO, NY, US). CHIAPAS: Nuevo Amatenango, 1,300 m, 17 July 1941, *Matuda 4724* (A, LL, MO, NY). COLIMA: without locality, 1–31 Dec. 1890, *Palmer 963* (GH, NY, US). DISTRITO FEDERAL: Tlalpam, July 1905, *Rose 8497* (GH, NY, US). DURANGO: 10 mi. N of Tamazula, deep canyon bottom, 1,500 ft., 19 Dec. 1939, *Gentry 5258* (GH, MO, NY). GUANAJUATO: San Miguel Allende, 9 Aug. 1947, *Kenoyer 1912* (A). GUERRERO: Mina, Manchon, ravine, 27 Sep. 1936, *Hinton 9597* (A, F, MO, US). HIDALGO: Valley of Tula, 8,300 ft., 10 Sep. 1899, *Pringle 8232* (A, F, GH, MO, NY, US). JALISCO: barranca near Guadalajara, 5,000 ft., 11 May 1901, *Pringle 8498* (F, GH, MO, NY, US); mountains N of Autlán, 1,500–1,650 m, 5 Oct. 1960, *McVaugh 19917* (GH, LL, NY, TEX, US). MEXICO: Temascaltepec, Bejucos, barranca, 6 Oct. 1934, *Hinton 6719* (A, F, GH, LL, US). MICHOACAN: vicinity of Morelia, Rincón, 1,950 m, 14 Aug. 1910, *Arsène 5494* (A, GH, MO, NY, US). MORELOS: 8 km NW of Oacalco on Hwy. 115D, 1,500 m, 2 Oct. 1983, *Anderson 12940* (MO, NY). NAYARIT: vicinity of Acaponeta, 9 Apr. 1910, *Rose 14210* (GH, NY). NUEVO LEON: 30 mi. S of Sabinas Hidalgo, Cuesta de Mamulique, 4 Apr. 1962, *Rivas 8154* (TEX). OAXACA: Oaxaca valley, 1 Oct. 1894, *Smith 638* (F, MO, NY). PUEBLA: Archeveche, 14 July 1907, *Arsène 1957* (US). QUERETERO: Cerro de las Campanas, 1,850 m, 9 July 1914, *Arsène 10058* (F, MO). QUINTANA ROO: 20 mi. S of Tihosuco, 4 Aug. 1972, *Webster 17681* (GH, MO). SAN LUIS POTOSI: Tamazunchale, 11 July 1937, *Edwards 482* (F, MO, NY, TEX). SINALOA: Villa Unión, Jan. 1895, *Lamb 399* (GH, MO, NY, US). TABASCO: Balancán, 12 Mar. 1975, *Novelo 74* (TEX). TAMAULIPAS: 10 km NW of El Progreso, 21 Aug. 1941, *Stanford 1005* (GH, MO, NY). VERACRUZ: al N de Orizaba, Cerro de Escamela, 15 Oct. 1966, *Rosas 66* (F, GH, LL, NY, US). YUCATAN: Lake Chichankanab, Apr. 1917, *Gaumer 23686* (F, GH, MO, NY, US). BELIZE. TOLEDO DISTRICT: Swasey Branch of the Monkey River, 24 Nov. 1941, *Gentle 3812* (A, LL, MO, US). STANN CREEK DISTRICT: All Pines, 5 ft., 23 Jan. 1930, *Schipp 708* (A, F, GH, MO, NY). WEST INDIES. BAHAMAS: Abaco Island, Allan's Cay, 6 Dec. 1904, *Brace 1527* (F, GH, NY). CUBA: without locality, without date, *Wright 2068* (MO, NY, US); Sierra de Anafe, Pinar del Río, 14 Dec. 1911, *Wilson 11297* (NY). JAMAICA: Walderston, Manchester, 2,600 ft., 1 Jan. 1918, *Harris 12863* (F, GH, MO, NY, US). TRINIDAD: Caroni River swamps, 1917, *Curran 1340* (US). VIRGIN ISLANDS: St. Thomas, Dec. 1928, *Nelthrop 3* (NY). GUATEMALA. ALTA VERAPAZ: 8 km below Tactic, along the Río Frío, 1,400 m, 1 Apr. 1941, *Standley 90542* (F, MO). BAJA VERAPAZ: Niño Perdido, bordering Río San José, 30 May 1977, *Lundell 21022* (LL). CHIMALTENANGO: Tecpam, 2,100 m, 3 Aug. 1933, *Skutch 541* (A, F, NY, US). CHIQUIMULA: 3–5 mi. N of Jocotán, Cerro Tixixi, 10 Nov. 1939, *Steyermark 31635* (F); 3–15 mi. NW of Chiquimula along Río Taco, between Chiquimula and Montaña Barriol, 26 Oct. 1939, *Steyermark 30615* (F). ESCUINTLA: NE of Escuintla, wooded barranca of Río Burrion, 720 m, 16 Mar. 1941, *Standley 89571* (F, MO). GUATEMALA: Guatemala, 1,480 m, 30 May 1923, *Ruano 405* (US). HUEHUETENANGO: San Miguel Acatan, 6,400 ft., 19 Aug. 1934, *Skutch 1021* (A, F, NY, US). IZABAL: vicinity of Quiriguá, 15–31 May 1922, *Standley 23857* (GH, NY, US). JUTIAPA: vicinity of Jutiapa, 850 m, 24 Oct.–5 Nov. 1940, *Standley 75248* (F, MO). PETEN: Santa Elena, entre carretera Turicentro y San Francisco, a 12 km, ca. 20 m lado sureste de la carretera, 9 Feb. 1972, *Ortíz 2244* (F, MO, NY). QUEZALTENANGO: Santa María de Jesús, Finca Pireneos, 1,350–1,380 m, 11 Mar. 1939, *Standley 68236* (F, NY). QUICHE: San Miguel Uspantan, Apr. 1892, *Smith 2920* (GH, MO, NY, US). RETALHULEU: region of Ajaxa, 330 m, 23 Feb. 1941, *Standley 88240* (F, MO). SACATEPEQUEZ: W of Alotenango, wooded slope on road to Escuintla, 3,200 ft., 3 Aug. 1965, *Breedlove 11413* (F, LL). SAN MARCOS: Tajumulco, NW slopes of Volcán Tajumulco, barrancas, 2,300–2,500 m, 25 Feb. 1940, *Steyermark 36553* (F). SANTA ROSA: Malpais, 4,000 pp., Nov. 1893, *Smith 6071* (GH, US). SOLOLA: San Pedro, between slopes of Volcán Santa Clara, 1,900–2,100 m, 6 June 1942, *Steyermark 47120* (A, F). SUCHITEPEQUEZ: near Patulul, 330–600 m, 5 Jan. 1939, *Standley 62146* (A, F). ZACAPA: Zacapa, 1 Jan. 1908, *Kellerman 7019* (F, NY, US). EL SALVADOR. AHUACHAPAN: without locality, 1921, *Padilla 197* (A, MO). LA UNION: vicinity of La Unión, 150 m or less, 13–21 Feb. 1922, *Standley 20809* (GH). MORAZAN: Montecristo, 140 m, 8 Dec. 1941, *Tucker 490* (US). SAN MIGUEL: Laguna de Olomega, 75 m, 20 Feb. 1922, *Standley 21021* (GH, US). SAN SALVADOR: without locality, Jan. 1922, *Calderón 121* (GH, MO, NY, US). SAN VICENTE: vicinity of San Vicente, 400–500 m, 7–14 Feb. 1947, *Standley 3573* (F). SONSONATE: vicinity of Sonsonate, 220–300 m, 18–27 Mar. 1922, *Standley 22300* (NY, US). HONDURAS. ATLANTIDA: vicinity of Tela, 0 m, 14 Dec. 1927–15 Mar. 1928, *Standley 53743* (A, F, US). CHOLUTECA: San Marcos de Colón, 6 June 1970, *Barkley 40510* (F, GH, MO). COMAYAGUA: 20 km al N de Siguatepeque, Barranco Trincheras, 1,400 m, 18 July 1962, *Molina 10840* (F, LL, NY, US). COPAN: 8 km de Santa Rosa de Copán, entre El Portillo y San Juan Opoa, 1,000 m, 23 Sep. 1963, *Molina 12882* (F, LL, NY). CORTES: San Pedro Sula, 1,000 pp., Sep. 1887, *Smith 5153* (GH, NY, US). DISTRITO CENTRAL: Suyapa, 10 July 1969, *Barkley 29429* (GH). EL PARAISO: road from Danlí to El Paraíso, 22 Feb. 1952, *Carlson 2517* (F). GRACIAS A DIOS: Río Lisiksa, 13 Nov. 1976, *Fryxell 2807* (F, NY). ISLAS DE LA BAHIA: Roatán Island, 4 km E of Coxenhole, 5–20 m, 21 Apr. 1967, *Molina 20701* (F, US). MORAZAN: Jicarito River, 2,600 ft., 18 June 1948, *Glassman 1652* (F, GH, TEX, NY). OCOTEPEQUE: NW of Ocotepeque, Mt. Cocal de Cordillera Merendón, 25 Aug. 1968, *Molina 22080* (F, NY). OLANCHO: 20 km NE de Juticalpa, Cerro El Boquerón, 700 m, 15 Jan. 1982, *Segovia 176* (NY). YORO: Quebrada Seca, 30 m, Dec. 1927, *Standley 53926* (A, F, US). NICARAGUA. BOACA: toward Camoapa, 200–500 m, 4 Apr. 1971, *Seymour 5426* (MO). CARAZO: N bank of Río Escalante, 6 km upstream from mouth, 24 Aug. 1977, *Neill 2438* (MO). CHINANDEGA: El Viejo, near Río Chiquito, 0–100 m, 27 Dec. 1969, *Seymour 2671* (MO). CHONTALES: 2.8 km N of Cuapa, 400–500 m, 21 Jan. 1978, *Stevens 6043* (MO); vicinity of Juigalpa, wet thicket along Río Paigua, 160 m, 4–13 June 1947, *Standley 9226* (F). COMARCA DEL CABO: Bilwaskarma, Thaler Memorial Hospital, pine woods, 9 July 1972, *Robbins 5777* (MO, NY, cultivated?). ESTELI: 6 km de Pueblo Nuevo, carretera a Limay cerro San Ramón, 810 m, 27 Sep. 1980, *Moreno 3094* (MO). GRANADA: Granada, Lake Nicaragua, 24 Dec. 1968, *Hamblett 1112* (F, GH, NY). JINOTEGA: 10 km NE of Jinotega, La Bastilla, 11 Jan. 1969, *Zelaya 2145* (F, NY). LEON: Momotombo, 27 July 1972, *Robbins 6110* (F). MADRIZ: Cerro Volcán de Somoto (Tepesomoto),

1,500–1,600 m, 16 Apr. 1980, *Araquistain 2122* (MO). MANAGUA: 12 km E of Managua, vicinity of Escuela Nacional de Agricultura y Ganadería, Route 1, 16 Jan. 1969, *Seymour 2235* (GH, MO, NY, cultivated?). MASAYA: without locality, 13 Feb. 1903, *Baker 163* (GH, NY, US). MATAGALPA: Cordillera Central de Nicaragua between Matagalpa and Jinotega, Santa María de Ostuma, 1,300–1,500 m, 8–15 Jan. 1963, *Williams 23401* (F, LL, US). NUEVA SEGOVIA: Ocotal, 7 Aug. 1977, *Stevens 3039* (MO). RIO SAN JUAN: near Cano Chotaleno, 20 km NE of El Castillo, 200 m, 18–21 Apr. 1978, *Neill 3582* (MO). RIVAS: Belén, K97, Route 2, 7 Jan. 1969, *Moore 1913* (GH, MO). ZELAYA: Madregava, rainforest on Mt. Liveco near Siuna, 19 Mar. 1971, *Nelson 5048* (MO); Punta del Mico, 0–100 m, 5 Mar. 1971, *Nelson 4248* (MO). COSTA RICA. ALAJUELA: Santiago de San Ramón, 26 Jan. 1937, *Brenes 21982* (F, NY). CARTAGO: 3 km SE of Cartago, 1,200 m, 10 Aug. 1967, *Taylor 4231* (MO, NY). GUANACASTE: along road from Santa Cruz to Playa Tamarindo near Río La Lima, 40–80 m, 28 Dec. 1966, *Burger 4113* (F, NY); Comelco Ranch 7 km NW of Bagaces, 8 May 1971, *Heithaus 87* (F, MO). HEREDIA: 5 km N of Puerto Viejo, along road to El Muelle, 100 m, 8 Jan. 1967, *Burger 4328* (F, MO, NY). LIMON: Los Diamantes on RR to Guapiles, Río Santa Clara, 6 Feb. 1957, *Carlson 3452* (F, US). PUNTARENAS: 4 mi. W of Rincón de Osa, forested area near the airfield, 4–7 June 1968, *Burger 5425* (F, NY); Monteverde, Oct. 1977, *Dryer 1662* (F, MO); Cabo Blanco Nature Reserve, 1–7 Dec. 1969, *Burger 6576* (F, LL). SAN JOSE: vicinity of El General, 1,040 m, Jan. 1936, *Skutch 2368* (A, GH, MO, NY, US); La Palma, 1,540 m, Aug. 1898, *Smith 7393* (F, GH, MO, NY). PANAMA. BOCAS DEL TORO: Water Valley, 9 Sep. 1940, *von Wedel 657* (GH, MO, US). CHIRIQUI: Burica Peninsula, 11 mi. W of Puerto Armueles in the vicinity of San Bartolo Límite, 19 Feb. 1973, *Liesner 71* (F, GH, MO); Borquete, in forest on slope of La Popa, 5,400 ft., 5 Aug. 1972, *D'Arcy 6408* (LL, MO, NY). COCLE: vicinity of El Valle, 800–1,000 m, 22 Dec. 1936, *Allen 91* (A, GH, MO). COLON: Salamanca, along stream 3 mi. E of Transisthmian highway on road to Salamanca, 100 m, 19 Dec. 1972, *Gentry 6735* (F, MO, NY). DARIEN: Tucuti, Chepigana, 5 Mar. 1940, *Terry 1386* (A, F, MO). HERRERA: hill above Chepo de las Minas, 700 m, 19 Dec. 1977, *Folsom 6979* (MO). LOS SANTOS: Las Tablas, 10 Aug. 1962, *Dwyer 2480* (MO, US). PANAMA: N of El Llano, 500–800 m, 25 July 1972, *Gentry 5573* (LL, NY). SAN BLAS: Comarca de San Blas, trail along Continental Divide, 25 July 1986, *McDonagh 368* (MO). VERAGUAS: Sona, 500 m, 24 Nov. 1938, *Allen 1045* (F, GH, MO, US). COLOMBIA. ATLANTICO: Barranquilla and vicinity, Tulara, Jan. 1928, *Elias 428* (US). BOLIVAR: vicinity of Turbaco, 200–300 m, 6–22 Nov. 1926, *Killip 14187* (GH, MO, NY). GUAJIRA: Maicao, Arroyo Tabaco near the Intercor Coal campamento at Tabaco, 9 Mar. 1981, *Bunch 0437* (HUA). SUCRE: trail from Coloso to Reserva de Primatas, 300–350 m, 17 Nov. 1981, *Gentry 34793A* (MO). GUYANA. Cultivated in British Guiana Botanic Gardens, Apr. 1907, *Jenman 8631* (BRG, cultivated). VENEZUELA. DISTRITO FEDERAL: around Caracas, 29 Apr. 1917, *Pittier 7121* (F, GH, US, cultivated). MIRANDA: San Diego de los Altos, 1,300 m, 24 June 1928, *Pittier 13014* (F, GH, NY, US, cultivated). OLD WORLD: FRENCH POLYNESIA. SOCIETY ISLANDS: Raiatea, Huaru, 31 Mar. 1927, *Moore 692* (MO, cultivated). INDIA. WEST BENGAL: Calcutta, Sibpur, without date, *Raizada 29153* (MO, cultivated). KENYA. Nairobi, Keren, Feb. 1963, *Gardner EAH, 12669* (US, cultivated). MALAYSIA. SARAWAK: Kapit, 1929, *Clemens 21029* (NY, cultivated). THAILAND. Bangkok, 1899, *Zimmermann 51* (MO, US, cultivated). VIETNAM. Da Nang, "ANNAM: Tourane," May–July 1927, *Clemens 4275* (MO, US, cultivated).

**1b. Malvaviscus arboreus** var. **drummondii** (Torrey & A. Gray) Schery, Ann. Missouri Bot. Gard. 29: 215. 1942. *Malvaviscus drummondii* Torrey & A. Gray, Fl. N. Amer. 1: 230. 1838. *Pavonia drummondii* (Torrey & A. Gray) Torrey & A. Gray, Fl. N. Amer. 1: 682. 1840. *Hibiscus drummondii* (Torrey & A. Gray) M. J. Young, Familiar Lessons in Botany with Flora of Texas 186. 1873. TYPE: United States. Texas: Austin Co., San Felipe de Tejas, *T. Drummond*, 1835 (Texas Drummond Coll. III, no. 1) (lectotype, selected here, NY [Torrey herbarium]; isolectotype, GH; probable isolectotype, NY).

Selection of a NY specimen from the Torrey collection as lectotype was necessitated by the absence of material at GH that might have been examined by either Gray or Torrey; the isotypes cited above were accessioned by GH well after *M. drummondii* was published.

It is unclear whether Young was describing *Hibiscus* as a new species, as a new combination after Torrey & A. Gray, or as a previously treated taxon. It is unlikely that Young intended to present a new species. Elsewhere in the flora Young's new species bear the notation "n. sp." The specimen described was certainly of Torrey & Gray's previously described *Malvaviscus drummondii* (red flowers, red fruit), and the identical specific epithet suggests Young was transferring the species to *Hibiscus*. However, Young did not cite Torrey & Gray as basionym authors and did not specifically state that *Hibiscus drummondii* was a new combination. Young did have at least indirect access to the *Flora of North America*; Torrey & Gray were cited elsewhere in the flora. However, many species that Torrey & Gray had named did not include an author citation. It seems possible that Young was simply unable to associate an author with what she thought was a legitimate name, *Hibiscus drummondii*.

*Malvaviscus arboreus* var. *drummondii* closely resembles variety *arboreus*, but the former plants are erect suffruticose, clone-forming, herbs or shrublets 0.5–1.5 m high; blades having mostly obtuse or rounded apices and abruptly cordate bases, the vestiture of petioles and peduncles densely and uniformly stellate-pubescent, the hairs

scarcely exceeding 0.25 mm. Chromosome number, $2n$ = ca. 14 pairs.

*Distribution (Fig. 1).* Sparsely occurring in northeastern Mexico and southern Texas along the Gulf Coast, but more widespread (albeit patchy) and numerous throughout central and eastern Texas, especially in rich soils along streams in shaded areas, cultivated or escaped from cultivation eastward to Florida; flowering all seasons, depending upon time, severity, and duration of frost conditions.

*Diagnosis and relationships.* According to Schery (1942), the variety *drummondii* "is one of the most distinct varieties of *M. arboreus*," which is an overstatement if one considers that he included within his concept of *M. arboreus* several taxa that others, including the present workers, would treat as distinct species. Actually, variety *drummondii* is a weakly differentiated, relatively uniform, populational complex of *M. arboreus*, which is largely restricted to central Texas. Southward along the Gulf coastal region of northeastern Mexico it appears to grade into variety *arboreus*, especially in the vicinity of Tampico, Mexico. Southward from Tampico variety *arboreus* becomes increasingly shrubby or clambering, the leaves less uniformly lobed, with mostly acute apices and a vestiture on the petioles and stems that is sparsely distributed, usually in lines, or sometimes glabrate or nearly so. Fryxell (1988) did not account for *M. arboreus* var. *drummondii* in his treatment of Mexico; the several specimens from Mexico that we cite here as belonging to variety *drummondii* are superficially similar to variety *arboreus* and, as indicated, the two taxa appear to intergrade in northeastern Mexico.

It is questionable whether variety *drummondii* is truly native to the states east of Texas, although it is certainly native to Texas, as attested to by the numerous and remarkably uniform populations that grow in central Texas. The taxon apparently was, early on, taken into cultivation in the more coastal southeastern United States. Collections in this area have been relatively isolated and are represented in Figure 1 as cultivated, whether known to be cultivated, thought to be persisting after cultivation, or thought to be escaped.

*Representative specimens examined.* UNITED STATES. ALABAMA: Tuscaloosa Co., University of Alabama campus, near Smith Woods, 25 July 1965, *Dermus 444* (GH, cultivated?). FLORIDA: Columbia Co., ca. 3 mi. N of U.S. 27 along Ichetucknee River, *Will*, 1961 (GH); Duval Co., near Jacksonville, without date, *Curtis s.n.* (GH, cultivated?); Escambia Co., Pensacola, *Brinker*, 1941 (MO, cultivated); Hillsborough Co., without locality, *Fredholm*, 1904 (GH, cultivated?); Leon Co., Tallahassee, live oak woods, 3 Oct. 1957, *Godfry 56118* (GH). GEORGIA: Daugherty Co., Albany, vacant lot by railroad yards, 5 Aug. 1947, *Thorne 5853* (GH, cultivated?). LOUISIANA: Rapides Parish, Alexandria, without date, *Hale s.n.* (NY, cultivated from Texas). MISSISSIPPI: Adams Co., near Natchez, without date, *Gale s.n.* (NY); Jackson Co., near Ocean Springs, 14 July 1889, *Fredholm 2176* (US); Lincoln Co., 11 mi. W of Brookhaven, 11 July 1950, *Webster 3281* (NY, US). TEXAS: Angelina Co., Neches River, *Boon*, 1934 (TEX); Aransas Co., Goose Island, N shore of Copano Bay, 10 June 1953, *Johnston 53175.27* (TEX); Bastrop Co., Bastrop State Park, 10 June 1953, *Gentry 1467* (NY); Bell Co., along Leon River channel, 5 July 1954, *York 54566* (TEX); Bexar Co., without locality, *Jermy*, 1904 (MO, NY); Brazoria Co., 4 mi. S of Angleton, 22 Oct. 1948, *Rogers 6579* (TEX); Brazos Co., College Station, 19 Sep. 1916, *Palmer 10756* (MO, US); Brown Co., 2 mi. E of Brownwood, along U.S. Hwy. 67, 3 Oct. 1965, *Wheat 10* (LL, cultivated); Burnet Co., Marble Falls, *Vanderbilt*, 1903 (US); Caldwell Co., Columbia, along streams, 1 Nov. 1899, *Bush 312* (MO, NY); Calhoun Co., 4 mi. NE of Tivoli, Guadalupe River bottoms, 24 Nov. 1945, *Cory 51153* (GH, NY, TEX); Cameron Co., near Brownsville, banks of the Rio Grande, 2 Aug. 1888, *Pringle 1959* (F, GH, NY, MO, US); Colorado Co., Eagle Lake, 21 Aug. 1946, *Warnock 46369* (TEX); Comal Co., Comanche Spring, Aug. 1849, *Lindheimer 685* (F, GH, MO, NY, TEX); Dallas Co., Dallas, *Reverchon*, 1879 (F); DeWitt Co., without locality, *Riedel*, 1941 (TEX); Fayette Co., Muldoon, 3 Oct. 1950, *Ripple 51-773* (TEX); Galveston Co., without locality, *Nelson*, 1941 (GH, TEX); Gillespie Co., Fredericksburg, without date, *Jermy 707* (MO); Goliad Co., Goliad, 22 Sep. 1926, *Williams 70* (F, MO); Gonzales Co., Ottine, woodland near bog on the Soefje farm, 3 Oct. 1943, *Barkley 13856* (F, GH, MO, NY, TEX); Grimes Co., Navasota, 1897, *Turner 2* (NY); Harris Co., Houston, 1 July 1872, *Hall 53* (F, GH, NY); Hays Co., San Marcos, *Tharp*, 1939 (F, GH, NY, TEX); Jackson Co., Navidad River, 1 July 1915, *Drushel 2844* (MO); Karnes Co., Green, Media Creek bottoms, 2 Sep. 1952, *Johnson 1004* (TEX); Kendall Co., Spanish Pass, 5 July 1911, *Clemens 609* (MO, NY); Kennedy Co., King Ranch, 6 mi. SE of headquarters, 23 Sep. 1958, *Lundell 15136* (LL, MO, NY); Lavaca Co., 18 mi. SE of Yoakum, along Hwy. 111, 16 July 1949, *Tharp 49167* (F, TEX); Limestone Co., N of Groesbeck, 18 Aug. 1968, *Fryxell 706* (F, MO); Madison Co., near Trinity River, 13–14 July 1909, *Dixon 441* (F, GH, NY); McLennan Co., Waco, without date, *Pace 221* (MO); Montgomery Co., Willis, Aug., *Warner s.n.* (MO); Nacogdoches Co., without locality, *Barrett*, 1944 (TEX); Nueces Co., Bishop, 20 June 1925, *Eifrig 19* (F); Refugio Co., Gulf Coast, "probably near Tivoli," July 1976, *Williams 454* (GH, MO); Robertson Co., 13 mi. E of Benchley, 28 July 1950, *Gould 5765* (TEX); San Patricio Co., Mathis, 26 Sep. 1958, *Correll 20414* (LL, NY); Travis Co., Harthaven, 6 Oct. 1944, *Warnock W1021* (F, NY, TEX); Tyler Co., 5 mi. NW of Woodville, roadside park, 28 Sep. 1948, *Cory 54840* (LL); Victoria Co., 8 mi. from Victoria, in field along Coletto Creek, 3 Oct. 1952, *Correll 14819* (LL); Walker Co., near Lake Livingston, 10 Aug. 1975, *Fryxell 2538* (NY); Washington Co., without locality, June 1938, *Brackett 175* (TEX); Wharton Co., Pierce, 14 Sep. 1901, *Tracy 7476* (F, GH, MO, NY, TEX); Wilson Co., Flo-

resville, June 1930, *Garza 2* (TEX). MEXICO. COAHUILA: Músquiz, *Hoult*, 1930 (TEX, possibly cultivated). TAMAULIPAS: San José, 18 Feb. 1939, *LeSueur 283* (F, TEX); vicinity of Tampico, 3–6 June 1910, *Palmer 525* (GH, US).

**2. Malvaviscus penduliflorus** DC., Prodr. 1: 445. 1824. *Malvaviscus arboreus* var. *penduliflorus* (DC.) Schery, Ann. Missouri Bot. Gard. 29: 233. 1942. *Malvaviscus arboreus* subsp. *penduliflorus* (DC.) Hadač, Folia Geobot. Phytotax. 5: 432. 1970. TYPE: Mexico. Without locality, date, or collector, Icones Florae Mexicanae no. 100 (Torner Coll. acc. no. 6331.1712, Hunt Institute, according to Fryxell, 1988).

*Malvaviscus penduliflorus*, except for its large corollas (mostly 5–6 cm long) and somewhat larger calyces (mostly 15–20 mm long), falls well within the descriptive parameters of *M. arboreus* var. *arboreus*. Chromosome number, $2n$ = ca. 84, 86.

*Distribution (Figs. 1–3).* *Malvaviscus penduliflorus* is a widespread cultivar of unknown origin. It is widely planted in gardens throughout the New World and escapes cultivation, to judge from information on herbarium labels. In addition, it is believed to hybridize occasionally with locally native taxa, mostly *M. arboreus*; flowering all seasons.

*Diagnosis and relationships.* *Malvaviscus penduliflorus* is remarkably uniform throughout its artificial range and is distinguished from *M. arboreus* var. *arboreus* by its larger corollas (mostly 50–60 mm long vs. 20–50 mm) and somewhat larger calyces (mostly 15–20 mm long vs. 10–15 mm). In addition, the leaves are nearly always ovate and subglabrous, and the flowers tend to be single and axillary with a pendulous nature. Its original habitat (or the area from which the "cultivar" might have arisen) is unknown, but it was first described by de Candolle from drawings made for the *Icones Florae Mexicanae* (cf. Fryxell, 1988), perhaps from garden material. As noted by Fryxell (1988), the species only rarely sets fruit, and this is verified by our own observations. Nevertheless, the area of origin of this species is probably south-central Mexico, for numerous collections from this region might reside within the descriptive parameters of *M. penduliflorus* except that the corollas tend to be shorter.

It is likely that *M. urticifolius* (= *M. hintonii*) is a white-flowered corolla form of *M. penduliflorus* with somewhat shorter petals, for as noted by Fryxell (1988), *M. hintonii* appears to be largely sterile and appears to occur in cultivation. We have, nevertheless, placed *M. hintonii* within the synonymy of *M. arboreus* var. *arboreus* because its leaf shape and vestiture more closely resemble that of *M. arboreus*. Certainly, it is not typical of material we include under *M. penduliflorus*. The corolla of *M. penduliflorus* is nearly always crimson or red; occasional specimens will have corollas that are pale pink (e.g., *Hu 12353A*, from Hong Kong, US), or "pure white" (*Plowman 11215*, Peru, F). It should also be noted that while the androecium is normally included within, or barely exceeding the corolla, as noted by Fryxell (1988), it is not uncommon to find the androecium extending beyond the corolla for 1–3 cm (e.g., *Cowan 4923*, TEX; *Hinton 13529*, LL; *Taylor 36*, TEX); at least this is true for our concept of this widespread, cultivated taxon.

We accept the likelihood that *M. hintonii* is a synonym of the earlier *M. urticifolius* (as treated by Fryxell, 1988), the latter having been first collected by Haenke, probably on his trip from Acapulco to Mexico City and return during the year 1791.

As noted under *M. arboreus* var. *arboreus*, it is likely that occasional hybridization between *M. arboreus* and *M. penduliflorus* occurs, at least to judge from seemingly intermediate specimens, most of these occurring in regions where both are known to occur near each other.

This is all discussed here to emphasize that the probable region of origin of the morphologically uniform cultivar *M. penduliflorus* is south-central Mexico, perhaps from the region south of Mexico City.

*Representative specimens examined.* UNITED STATES. FLORIDA: Dade Co., Miami, 24 Dec. 1927, *Moldenke 3581* (NY, cultivated); Hendry Co., Clewiston, 4 May 1958, *Cooley 6231* (NY); Hillsborough Co., Auburn Highlands, July 1970, *Burch 3755* (MO, cultivated); Lee Co., East Fort Myers, apparently escaped, *Moldenke 993* (MO, NY, US); Manatee Co., Palmetto, 31 July 1970, *Burch 3757* (MO, cultivated); Palm Beach Co., Delray Beach, edge of coastal sand dune thickets, 29 Dec. 1966, *Moldenke 24176* (LL); Seminole Co., 1.4 mi. W of Sanford city limit, grassy thicket near Florida Hwy. 46, escaped but not actively spreading, 24 Sep. 1960, *Ward 2240* (GH, US); Volusia Co., Ponce Inlet, grassy soil on edge of salt marsh, 4 Oct. 1981, *Correll 52747* (NY). HAWAII: Oahu, Mokuleia, 30 July 1937, *Degener 11402* (GH, MO, NY, cultivated). TEXAS: Bosque Co., Clifton, 16 June 1925, *Eifrig 15* (F); Brazos Co., College Station, flowerbed, S side Hart Hall, (Texas A&M University) campus, 22 Nov. 1948, *Trew 162* (TEX, cultivated); Cameron Co., Brownsville, 21 Dec. 1919, *Hanson 36* (GH, MO, NY, cultivated); Harris Co., Houston, Teas Nursery, 5 Dec. 1933, without collector (TEX, cultivated); Webb Co., Laredo Jr. College Campus, 11 Nov.

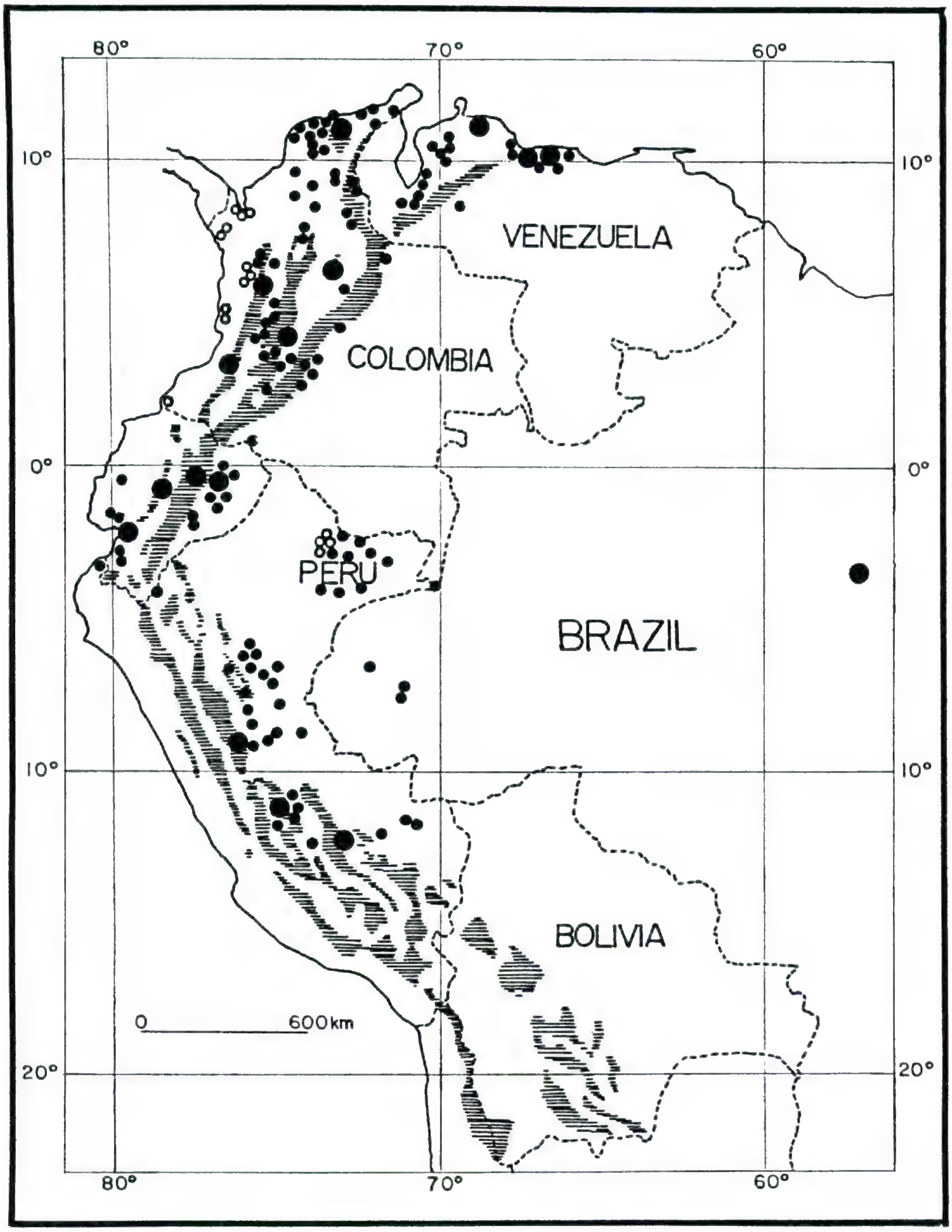


FIGURE 3. Distribution of *Malvaviscus concinnus* (small closed circles), *M. penduliflorus* (large closed circles), and *M. williamsii* (small open circles) in South America.

1962, *Garcia 28* (TEX, cultivated); Willacy Co., 5 mi. W of Raymondville, 18 Apr. 1965, *Rios 273* (LL, cultivated). MEXICO. CHIAPAS: Tenejapa, near the school house of Pokolum, paraje of Sibanilha, 5,200 ft., 15 July 1965, *Breedlove 11048* (F, LL). CHIHUAHUA: Llano Grande, 19 May 1960, *Pennington 151* (TEX). GUANAJUATO: Guanajuato, 1891, *Dugès 280* (GH, cultivated). GUERRERO: Atoyac de Alvarez, 1,000 m, 19 Dec. 1984, *Cowan 4923* (TEX). MEXICO: Temascaltepec, Tenayac, 1,450 m, 8 June 1933, *Hinton 4014* (A, NY, US). MICHOACAN: Zitácuaro, La Mora, 1,300 m, 12 Dec. 1938, *Hinton 13529* (GH, LL, NY, US). MORELOS: near Cuernavaca, 5,500 ft., 28 Aug. 1935, *Bailey 305* (F). NAYARIT: 6.5 mi. E of Jalcocotán, 800–1,200 m, 9 Sep. 1960, *McVaugh*

*18932* (NY, TEX, US). NUEVO LEON: on I.T.E.S.M. campus, 1,700 ft., 28 July 1970, *Taylor 36* (TEX, cultivated). OAXACA: Santo Domingo, 1,600 m, 22 Dec. 1906, *Conzatti 1683* (F). PUEBLA: Cuetzalán, 940 m, 4 Mar. 1976, *Baez 275* (F). SAN LUIS POTOSI: Mpio. San Antonio, El Lejem, 15 Dec. 1978, Alcorn *2260* (TEX, cultivated). SINALOA: vicinity of Mazatlán, 7 Apr. 1910, *Rose 14156* (NY, US, cultivated). VERACRUZ: 2 km S of Tampico, 23–31 May 1910, *Palmer 391* (MO); near Córdoba, 20 July 1941, *Schery 188* (MO). BELIZE. St. Johns College Grounds, 15 May 1970, *Dieckman 237* (MO, cultivated). WEST INDIES. BAHAMAS: northern Bimini Island, Lerner Lab, 6 May 1948, *Howard 10226* (GH, NY, US, cultivated). CUBA: Sierra Maestra, 30 km S of Bayamo, 400 m, 17 Aug. 1951, *Webster 4123* (GH, US). CURAÇAO: at pool St. Martha, Jan. 1970, *Arnold-Broeders 3888* (A). DOMINICAN REPUBLIC: Peravia, El Taton, 13.7 km E de San José de Ocoa en la carretera a La Laguna, 20 Oct. 1982, *Mejia 23795* (NY). GUADELOUPE: Basse Terre, 25 Mar. 1982, *Howard 19775* (NY, cultivated). JAMAICA: St. Andrew, U.C.W.I. campus, 550 ft., 30 Oct. 1957, *Yuncker 17241* (NY, cultivated). PUERTO RICO: Barranquitas, along Hwy. 156, 6.0 mi. SW of Comerío, 4.7 mi. SW of junction with Hwy. 776, 25 Nov. 1981, *Hansen 9335* (MO). ST. LUCIA: Canaries River approaching Morne Gimie, 28 Jan. 1985, *Howard 19935* (A, NY). TORTOLA: Treasure Isle Hotel grounds, 10 m, 15 Dec. 1965, *D'Arcy 387A* (MO, cultivated). TRINIDAD AND TOBAGO: I.C.T.A. Savanna, 23 Feb. 1959, *Richards 1378* (NY). HONDURAS. ATLANTIDA: vicinity of La Ceiba, near Puente Alto stop on S.F. Co. RR, 800 ft., 19 July 1938, *Yuncker 8523* (F, GH, MO). COMAYAGUA: vicinity of Siguatepeque, 1,050 m, 25 Mar.–5 Apr. 1947, *Standley 6658* (F, cultivated). MORAZAN: Zamorano, 800 m, Feb. 1945, *Rodriguez 2264* (F). NICARAGUA. ZELAYA: vicinity of Puerto Cabezas, 11 Feb. 1977, *van Stelle 18* (MO). COSTA RICA. SAN JOSE: San José, grounds of Nacional Museum, 1,140 m, 13 Dec. 1966, *Meyer 10021* (MO, cultivated). PANAMA. CHIRIQUI: El Hato del Volcán, fencerows and old citrus grove around hotel, 1,390 m, 5 Jan. 1975, *Nee 14143* (MO). COCLE: near El Cope, 27 Oct. 1967, *Garner 39* (A). COLOMBIA. ANTIOQUIA: Medellín, Ciudad Universitaria U. de A., 6 Aug. 1981, *Alzate 13* (HUA). CUNDINAMARCA: valley above Colegio, 800 ft., 5 July 1968, *Barkley 38852* (TEX). SANTANDER: 17 km SE of San Vicente de Chucuri on road to Zapatoca, 1,250 m, 25 July 1975, *Gentry 15438* (MO, NY). VALLE DEL CAUCA: Palmira, 1,100 m, 2 Jan. 1972, *Maas 576* (MO); Calí, Universidad del Valle Zona de residencias, 26 Nov. 1982, *Paz 12* (MO). VENEZUELA. ARAGUA: Maracay, Agronomia, Universidad Central de Venezuela, 24 June 1963, *Trujillo 5709* (F, cultivated). DISTRITO FEDERAL: Caracas, Colinas de El Paraíso, Jan. 1944, *Lasser 1025* (US). MIRANDA: Parque Nacional Guatopo, 24 km NNW of Altagracia de Orituco, along Quebrada Agua Blanca, 350 m, 23 Aug. 1979, *Nee 17718* (F). BRAZIL. AMAZONAS: Maués, avenue facing river, cultivated, 1983, *Hill 13204* (R). PARAIBA: Areia Escola de Agronomia do Nordeste, 25 Oct. 1944, *Vasconcellos 177* (RB). RIO DE JANEIRO: Rio de Janeiro, Estrada da Vista Chinesa km 2, Alto da Boa Vista, 3 Sep. 1979, *Carauta 3183* (F). SÃO PAULO: Limeira, *Hoehne*, 1946 (SP). ECUADOR. COTOPAXI: 1.9 km NW of El Corazon, road between Quevedo and El Corazon, 1,225 m, 5 Apr. 1983, *Croat 55836* (MO, NY); near La Mana, islet in Río San Pablo, 500 ft., 18 July 1978, *Webster 22724* (TEX). GUAYAS: Guayaquil, 0–20 m, 1964, *Valverde 680* (US); Capeira, km 21 Guayaquil to Daule, 17 Sep. 1982, *Dodson 11280* (MO). LOS RIOS: km 56 Quevedo–Santo Domingo, Río Palenque Biological Station, 150–220 m, 31 Mar. 1971, *Dodson 4290* (F, MO). NAPO: Puerto Napo, 7 km S of Tena, 8 Aug. 1988, *Mendenhall 15* (TEX, cultivated). PERU. CUZCO: La Convención, Quillabamba, Salaspampa, road to Kiteni, chacra del Sr. Alejo Daniel Caceres, Río Urubamba, 1,110 m, 28 Oct. 1986, *Nuñez 6320* (MO). HUANUCO: Tingo María, Río Huallaga, 12 Mar. 1977, *Boeke 1229* (MO, NY); Jardín Botánico de Tingo María, 670 m, 8 Dec. 1981, *Plowman 11215* (F, cultivated). JUNIN: N of La Merced, 12 km N of Puente Paucartambo, Río Paucartambo, chacra Schuler, 960 m, 6 Feb. 1979, *Teppner 79/318* (US). OLD WORLD: EGYPT. Cairo, Cairo University garden, 28 Aug. 1974, without collector (LL, MO, cultivated). FRENCH POLYNESIA. MOOREA: Faatoai Valley, usually cultivated but beginning to escape in areas of deserted dwellings, 19 July 1967, *Smith 103* (MO, NY, US). INDIA. UTTAR PRADESH: Dehra Dun, Forest Research Institute, *Raizada*, 1954 (NY, cultivated); Lucknow, Central Drug Research Institute, 113 m, 26 Apr. 1982, *Parsad 11769* (F, cultivated). PAKISTAN. SIND: Karachi, National College, 6 Aug. 1969, *Abedin 3777* (NY, US, cultivated). PAPUA NEW GUINEA. MANUS ISLAND: Pelikawa Village, 25 June 1971, *Stone 10494* (A, cultivated). PHILIPPINES. LUZON: Manila, Jan. 1954, *Steiner 332* (US, cultivated). MINDANAO: Davao, valley near Santa Cruz, 900 ft., *A.N.U. 1587* (A). SOCIETY ISLANDS. TAHITI: Punaauia, Outumaoro, Hotel Maeva, 3 m, 2 Feb. 1983, *Florence 4473* (NY, cultivated). TAIWAN. Pingtung city, 29 Sep. 1976, *Ching-en Chang 9417* (MO, cultivated). TANZANIA. Kibaha, 14 Nov. 1970, *Flock 710* (MO, cultivated). WESTERN SAMOA. UPOLU ISLAND: Moto'otua in the Apia area, 2 Jan. 1975, *Whistler W2006* (US, cultivated).

**3. Malvaviscus achanioides** (Turczaninow) Fryxell, Syst. Bot. 4: 253. 1979. *Abelmoschus achanioides* Turczaninow, Bull. Soc. Imp. Nat. Moscou 31: 196. 1858. *Hibiscus achanioides* (Turczaninow) Hemsl., Biol. Centr. Amer., Bot. 1: 121. 1879. TYPE: Mexico. Tabasco: "in sylvis Teapae," 2,000 ft., *Linden 838* [*938*] (holotype, not located; photoisotype, F).

*Malvaviscus cutteri* Standley, Publ. Field Columbian Mus., Bot. Ser. 4: 315. 1929. TYPE: Honduras. Atlantida: Lancetilla Valley near Tela, Dec. 1927–Mar. 1928, *Standley 54127* (holotype, F; isotypes, A, US).

Shrub or small tree 1–4 m high. Stem densely pilose, the hairs 1–2 mm long. Leaves mostly 15–35 cm long, 5–20 cm wide, scarcely reduced upward; petioles 3–15 cm long, pilose like the stem; blades broadly ovate to cordate, rarely weakly lobed, pubescent on both surfaces, especially along the major veins, the margins irregularly serrate, undulate, to nearly entire. Flowers mostly 1–7 in short terminal subfasciculate clusters, or rarely 20–30 in an abbreviated panicle, the peduncles mostly 0.5–3.0 cm long. Calyces mostly 16–22 mm long, pilose, yellowish, the subtending bracts 8–11 and

about ½ as long at the calyx. Corollas 4–5 cm long, red, not flaring, petal apices occasionally lobate. Fruit ca. 15 mm across, fleshy, and red.

*Distribution (Fig. 1).* Eastern Honduras to Mexico, along the lower montane slopes and adjacent flood plains of the Gulf coastal regions, mostly evergreen rainforests, 100–1,000 m; flowering October to January.

*Diagnosis and relationships.* The large leaves, which are scarcely reduced upward along the stem, pilose vestiture, and large calyces distinguish this species from the more typical elements of *M. arboreus*. In vegetative characters, and because of its large yellowish calyces, it approaches *M. concinnus* of South America, but in most other traits it is like *M. arboreus*.

Specimens from Honduras, which have been called *M. cutteri*, have somewhat larger, thinner, more cordate, leaves than specimens from Mexico; otherwise these are quite similar. Occasional specimens from the more montane Pacific slopes of western Chiapas (e.g., *Matuda 5357*, Boquerón, ca. Motozintla, 2,540 m, LL), and perhaps some of those examined by Fryxell (1988) but not examined by us, resemble *M. achanioides* in vestiture and leaf shape, but in other characters they more nearly approach *M. arboreus* (e.g., the corollas are quite short, ca. 30 mm long, and tend to flare) and we have placed such collections in the latter, believing the pubescence and larger leaves to be convergent characters in this area.

An alternative treatment might include all of *M. achanioides* within an expanded *M. arboreus*, but that would also collapse the more artificially maintained *M. penduliflorus*. In short, we have maintained a nomenclature that is both traditional and pragmatic, though imperfect if one considers the character variations found in the occasional populations, which tend to blur the specific lines proposed.

Finally, except for its somewhat smaller calyces and less flaring, somewhat shorter corollas, *M. achanioides* is similar to the more southern *M. concinnus*, and some future workers might opt to treat the former as part of the latter complex.

*Additional specimens examined.* MEXICO. CHIAPAS: Mpio. Ixtacomitán, stream above Ixtacomitán, 455 m, *Breedlove 56796* (LL, NY). TABASCO: Mpio. Teapa, Cerro del Cocona, 3 km from Teapa, 26 Oct. 1980, *Cowan 3318* (F, MO, NY, TEX); Grutas del Cocona, ca. Teapa, 18 Nov. 1979, *Ramos 2696* (NY). VERACRUZ: 5 km E of Tebanca (5 km E of E side of Lago Catemaco), 830 m, 15 Jan. 1981, *Nee 19971* (F). GUATEMALA. *Martínez et al. 23588* (MO). HONDURAS. ATLANTIDA: Lancetilla Valley near Tela, 6 Dec.–20 Mar. 1928, *Standley 52756* (A, F, US).

4. **Malvaviscus concinnus** Kunth, Nov. Gen. & Sp. 5: 286. 1822. *Achania concinna* (Kunth) Sprengel, Syst. Veg. ed. 16, 3: 100. 1826. TYPE: Ecuador. Loja: "Crescit prope Loxam Peruvianorum," *Humboldt*, 1802 (holotype, P-HBK not seen; photoisotype (from Berlin), F, GH).

*Malvaviscus balbisii* DC., Prodr. 1: 445. 1824. TYPE: Brazil (according to Index Kewensis). Without locality, without collector (holotype, G-DC, microfiche (single leaf only)).

*Malvaviscus cordatus* Balbis ex DC., Prodr. 1: 445. 1824. nomen nudum (merely listed by de Candolle as synonymous with *M. balbisii* DC.).

*Malvaviscus populifolius* C. Presl, Reliq. Haenk. 2: 135. 1853. TYPE: "In terris occidentalibus Mexici," without date, *Haenke s.n.* (holotype, PR not seen; photoholotype TEX, from negative in possession of Fryxell, who graciously loaned the same).

Fryxell did not account for this name in his Mexican treatment but noted that the type material does "not conform to anything I have seen from Mexico" (pers. comm.). We agree with this observation and believe that the type concerned, on morphological grounds, is best placed with *M. concinnus*, thinking that Haenke probably collected the material in Central or South America, but subsequently mislabeled as from Mexico, as also suggested by Fryxell (pers. comm.).

*Malvaviscus elegans* Linden & Planchon, Pl. Columb. 1863. TYPE: Venezuela. Trujillo: La Pena, 1,675 m, ca. 1846, *Schlim 751* (holotype, BR not seen; photoisotype, F).

This tome (*Plantae Columbianae*) was not effectively published until ca. 1875, according to Sprague (1927). The name, however, was only questionably published at that time, there being only five copies produced for distribution and these without knowledge of the authors concerned. Guerke (1892) took up the name, and one might give the latter date as the point of effective publication.

*Malvaviscus funckeanus* Linden & Planchon, Pl. Columb. 1863. TYPE: Venezuela. Distrito Federal: Caracas, La Cumbre, without date, *Funck 372* (holotype, BM not seen).

See discussion after *M. elegans*, above. Guerke (1892) took up this name for his *Flora Brasiliensis* treatment.

*Malvaviscus speciosus* Linden & Planchon, Pl. Columb. 1863. TYPE: Venezuela. Mérida: forests, 1,950 m, Aug. 1842, *Linden 354* (holotype, BM not seen; photoisotype, F).

See discussion after *M. elegans*, above.

*Malvaviscus spathulatus* Garcke in Otto & Dietr., Allg. Gartenzeitung 21: 321. 1853. TYPE: Costa Rica. *Oersted 407* (holotype, B destroyed?; photoholotype, F-9429; isotype, C not seen; photoisotype, F-21598).

*Malvaviscus longifolius* Garcke in Otto & Dietr., Allg. Gartenz. 22: 321. 1854. TYPE: cultivated in Erfurt, Germany, from seed collected in northern Peru,

*Warszewicz s.n.* (holotype, B destroyed?; photoholotype, F-9427).

*Malvaviscus cuspidatus* Turcz., Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 31: 190. 1858. SYNTYPES: Venezuela. Caracas: La Cumbre, *Funck 350* (specimen not located); Caracas, La Cumbre, *Funck* [*Galeotti*] *372* (syntypes, G not seen, P not seen; photosyntype, F-23715, according to Fryxell, 1988).

*Malvaviscus oligotrichus* Turcz., Bjull. Moskovsk. Obšč. Isp. Prir., Otd. Biol. 31: 190. 1858. *Malvaviscus glabrescens* Planchon & Linden ex Triana & Planchon, Ann. Sci. Nat. (Paris) 17: 168. 1862, nom. superfl. TYPE: Colombia. Norte de Santander: Ocaña, 1850, *L. Schlim 105* (isotype, G not seen; photoisotype, F).

*Malvaviscus leucocarpus* Planchon & Linden ex Triana & Planchon, Ann. Sci. Nat. (Paris) 17: 169. 1862. TYPE: Colombia. Sativa, Cordillera Oriental, *Triana 5278/3* (lectotype, P not seen; isolectotype, COL not seen, according to Fryxell).

See: Bol. Soc. Argent. Bot. 8: 101. 1960.

*Malvaviscus velutinus* Planchon & Linden ex Triana & Planchon, Ann. Sci. Nat. (Paris) 17: 168. 1862. TYPE: Colombia. Tolima: Maraquita, "Entre la Mesa et El Espinal, bassin du Magdalena," 400–1,200 m, Jan. 1854, *Triana 3132* (holotype, P not seen; isotypes, NY not seen, US not seen; according to Fryxell, pers. comm.).

*Malvaviscus guerkeanus* Hieron., Bot. Jahrb. Syst. 21: 320. 1895. TYPE: Colombia. Low wet areas along Río Magdalena, Mar. 1868, *A. Stuebel 106b* (lectotype, B destroyed?; isolectotypes, F, GH).

*Malvaviscus maynensis* Huber, Bol. Mus. Paraense Hist. Nat. 4: 583. 1906. TYPE: Peru. "Cerro de Canchahuaya," Quebrada de Cerrado, 27 Oct. 1898, *J. Huber 1383* (holotype, MG; photoholotype, F; isotype, R).

*Malvaviscus integrifolius* Ulbr., Verh. Bot. Vereins Prov. Brandenburg (1908) 88. 1909. TYPE: Brazil. Amazonia: "bei Humaytha am oberen Juruá," 22 Apr. 1901, *E. Ule 5444* (holotype, B destroyed?; fragment holotype, R; photoholotype, F, GH; photoisotype, US).

*Malvaviscus ulei* Ulbr., Notizbl. Königl. Bot. Gart. Berlin 6: 328. 1915. TYPE: Brazil. Amazonia: "Alto Acre bei Seringal Auristella," June 1911, *Ule 9591* (holotype, B destroyed?; photoholotype, GH).

Shrubs, small trees, or clambering vines, mostly 1–8 m high. Leaves broadly ovate to cordate, densely pubescent to subglabrous, the vestiture uniformly short and variously spaced to long and closely packed so as to appear velutinous. Flowers single and axillary, or in terminal aggregations, the peduncles 1–10 cm long. Calyces mostly broadly campanulate at maturity, 18–40 mm long, 10–30 mm wide, variously pubescent, as noted in the discussion below, the subtending bracteoles mostly 10–20, filiform to linear-lanceolate (1–3 mm wide), if the latter, nearly always broadest at or near the base. Corollas pale pink to dark red, usually broadly flaring at anthesis, mostly 40–70 mm long, rarely less, broadly to sometimes narrowly oblanceolate, usually at least a few petals with some degree of apical lobing, rarely not. Style and staminal column mostly protruding from the corolla for 10–40 mm. Fruits large and fleshy, red or white, mostly 15–30 mm wide at maturity, the seeds large, ovoid, up to 10 mm long and 4 mm wide.

*Distribution (Figs. 1, 3).* Northwestern South America along the upper tributaries of the Amazon River in Peru, Ecuador, Colombia, Venezuela, Brazil, Panama, and Costa Rica, from 100 to 2,000 m, often in lower montane cloud forests; flowering all seasons.

*Diagnosis and relationships. Malvaviscus concinnus* is an extremely variable species throughout its range, often over very short distances, the variation being much like that found in *M. arboreus* in North America. Thus, collections from San Martín, Peru, may possess a minutely stellate-pubescent vestiture (0.2 mm high or less) upon the calyces and associated bracts (*Klug 3919*, F, GH, MO, NY, US), or the vestiture may be quite pronounced or hirsute-stellate (0.5–1.5 mm high) on these same organs (*Schunke-Vigo 7767*, MO, US), and intermediates between these extremes may also occur (*Schunke-Vigo 6898*, MO, US). The corolla length and degree of apical flaring are quite variable: among the specimens just cited, and others from San Martín, the length varies from ca. 42 mm (*Schunke-Vigo 6898*, MO, US) and not so widely flaring (4 cm across), to ca. 65 mm (*Allard 22074*, US) and markedly flaring (to 9 cm across).

Variation from population to population is especially apparent along the upper, more western, tributaries of the Amazon River basin from Venezuela, Colombia, Ecuador, and Peru eastward to 70°W longitude. Thus, the names *M. elegans*, *M. oligotrichus*, *M. longifolius*, and *M. maynensis* have been applied to forms with broadly lanceolate leaves; *M. velutinus* to forms with a vestiture of densely packed, long-stellate hairs; *M. integrifolius* and *M. ulei* to forms with nearly entire leaves, the latter having somewhat shorter petioles and longer calyces; and *M. speciosus* with trilobed, cordate leaves. In all of the aforementioned type material, as well as among the representative specimens cited, there is considerable variation in leaf shape, corolla size, vestiture, and fruit dimensions, so much so that one is forced to the conclusion that there exists in South America a single widespread, highly variable species, *M. concinnus*, and a more localized, more readily recognized, relatively uniform species, *M. williamsii*. The latter might have been treated, with equal validity, as a variety of *M. concinnus*. But *M. williamsii* is much

better delimited than variety *drummondii*, the only infraspecific taxon maintained under *M. arboreus*, and it is certainly better delimited than *M. achanioides*.

Some comments on the large white fruits occasionally found in *M. concinnus* seem in order. Such fruits in North America are mostly confined to Panama and Costa Rica, where they are usually associated with plants having large cordate leaves; however, similar fruits also occur on elliptical-leaved specimens from Costa Rica that have been called *M. palmanus* (e.g., *Burger 5425*, F, NY; *Burger 5492*, F, NY; *Burger 7228*, F, GH), but which we include in *M. arboreus*. White fruits, though smaller than those found in Central America, occasionally occur on Mexican plants referable to typical *M. arboreus*. Thus, fruit color (the basis for the name *M. leucocarpus*), like leaf shape and vestiture, is variable and cannot be used alone for delimitation.

*Representative specimens examined.* PANAMA. COCLE: El Cope, E of sawmill above El Cope, 2,300 ft., 27 July 1978, *Hammel 4096* (MO). DARIEN: lower slopes of Alturas de Nique along Río Coasi, 26 Dec. 1980, *Hartman 12258* (MO). PANAMA: N of El Llano, 500–800 m, 25 July 1972, *Gentry 5573* (F, MO). VERAGUAS: near Sante Fé, road at base of Cerro Tute, 3,000 ft., 18 Sep. 1979, *Antonio 1899*, 1901 (MO). COSTA RICA. ALEJUELA: between Cañas and Upala, 4 km NNE of Bijagua, ca. 400 m, 24 June 1976, *Croat 36309* (MO); San Carlos, márgen del Río Peñas Blancas, 29 June 1985, *Haber 1756* (MO). HEREDIA: Finca La Selva, OTS Field Station along the Río Puerto Viejo, just E of the junction with the Río Savapiquí, ca. 100 m, 29 Nov. 1982, *McDowell 995* (LL, TEX), 3 Dec. 1982, *McDowell 1028* (MO); Tirimbina, 700 ft., 1 June 1971, *Proctor 32220* (LL). COLOMBIA. AMAZONAS: east bank of Amazon River ca. 3 mi. N of Leticia, 27 Jan. 1969, *Croat 7566* (MO). ANTIOQUIA: Cordillera Central Boquerón, ca. 16 km NW of Medellín on road to Turbo, 6°20′N, 75°40′W, 2,500–2,600 m, 10 Jan. 1986, *Stein 3160* (MO). ATLANTICO: region de Barranquilla, llanada de Juanmina, 10 m, 15 Jan. 1961, *Dugand 5499* (NY). BOLIVAR: near Cartagena, La Popa, 50–175 m, 2 Nov. 1926, *Killip 14052* (A, GH, NY). BOYACA: Valle de la Uvita, near Uvita, 2,490–2,560 m, 16 Sep. 1938, *Cuatrecasas 1850* (F, US). CESAR: La Jagua, Magdalena Valley, 5 Sep. 1924, *Allen 565* (F, MO). CUNDINAMARCA: Mpio. La Mesa, carretera de La Mesa a Anapoima, 1,300 m, 14 May 1952, *Fernández 1336* (NY, US). GUAJIRA: N slopes of Cerro del Espejo Serranía de Perija, Venezuela border, 10°28′N, 72°50′W, 2,550 m, 28 Apr. 1987, *Gentry 57192* (MO). HUILA: 1 km S of Villavieja, E of Río Magdalena, 400 m, 21 July 1950, *Smith 1241* (GH, US). MAGDALENA: Las Nubes, Sierra del Libaus, 4,500–6,000 ft., 15 Dec. 1898–23 Jan. 1899, *Smith 734* (several individuals and specific localities under this number) (A, F, GH, MO, NY). META: Río Guejar, S of El Mico Airstrip, 400 m, 7 Nov. 1949, *Philipson 1372* (F, US). PUTUMAYO: Umbria, 0°54′N, 76°10′W, 325 m, Oct.–Nov. 1930, *Klug 1712* (A, F, MO). SANTANDER: vicinity of Las Vegas, 2,600–3,000 m, 21–23 Dec. 1926, *Killip 16087* (A, GH, MO, NY, US). SUR DE SANTANDER: vicinity of Barranca Berjema, Magdalena Valley between Sogamoso and Colorado rivers, 100–500 m, 20 Jan. 1935, *Haught 1532* (F). TOLIMA: Armero, Valle del Río Magdalena, 400 m, 6 Oct. 1940, *Cuatrecasas 10496* (F, MO, NY, US). VENEZUELA. ARAGUA: subida de Las Vueltas, Parque Nacional, 1,300 m, Aug. 1947, *Pittier 15.519* (US). CERRO EL AVILA: Quebrada Quintero, 1,600 m, *Manara*, 1976 (NY). DISTRITO FEDERAL: Camino de ronda Las Flores a Papelón (Guayabal), 23 Aug. 1939, *Delgado 271* (F, US); near Caracas, between Cotiza and Los Venados, Oct. 1924, *Albert 76* (US); vicinity of Caracas, Chacaito Gorge, 800–1,000 m, 24 Aug. 1923, *Pittier 1116* (A, GH, NY, US). LARA: hacia la Estación Experimental del Ministerio de Agricultura y Cría en Sanare, 1,500 m, Aug. 1959, *Aristeguieta 3943* (F). MERIDA: Río Gonza, La Isla Jaji, 1 Nov. 1968, *López-Palacios 1918* (NY). MIRANDA: E of Quebrada Serraduro, E of Hacienda Garate, 16 km NE of Caucaguito, 30 km NE of Petare, between Petare and Guarenas, 1,200–1,500 m, 6 Oct. 1963, *Steyermark 91616* (GH). PORTUGUESA: Pozo Blanco, estación lluviosa, 2 Oct. 1979, *Ortega 804* (MO). TACHIRA: Quebrada Agua Azul, S of El Reposo, 14 km SE of Delicias, 7°31′N, 72°24′W, 2,150–2,300 m, 22–23 July 1979, *Steyermark 11874* (MO). ECUADOR. CHIMBORAZO: Sibambe, Hacienda "La Carmela," 100–1,600 m, 16 Aug. 1943, *Solís 5349* (F). ESMERALDAS: between Tonchigue and Galera, Esmeraldas–Muisne Road, 23 Nov. 1980, *Harling 16693* (F). GUAYAS: 12 km W of Guayaquil, Hacienda Barcelona Trasil, 4 Apr. 1962, *Gilmartin 667* (US). MANABI: above Noboa, 200 m, 19 July 1942, *Haught 3413* (GH, NY, US). MORONA–SANTIAGO: Parroquia Cumanda, Río Pastaza, ca. 4 km W of Mera, 23 Aug. 1968, *Lugo 355* (F, NY). NAPO: Río Gueppi (tributary of Río Putumayo), below Peruvian border post of Puerto Peru, 200 m, 15 May 1978, *Gentry 21871* (F, MO). EL ORO: Sitio denominado pénjamo, 100 ft., 23 Nov.–16 Dec. 1978, *Escobar 824* (HUA, TEX); between Santa Rosa and La Chorita, 0–100 m, 27 Aug. 1923, *Hitchcock 21141* (NY, US). PASTAZA: Puyo–Tena road, 4.5 km from Puyo, ca. 900 m, 8 July 1980, *Sobel 2452* (NY). SANTIAGO–ZAMORA: E slope of the cordillera, valley of the Ríos Negro and Chupianza on the trail from Sevilla de Oro to Méndez, 1 Nov. 1944, *Camp E-829* (US). PERU. AYACUCHO: Estrella, between Huanta and Río Apurimac, 500 m, 8 and 14 May 1929, *Killip 23065* (F, NY, US). HUANUCO: Leoncio Prado, La Divisora, Cordillera Azul near border with Ucayali, 1,620–1,760 m, 75°48′W, 9°05′S, 10 Aug. 1980, *Gentry 29567* (F, MO); Pachitea, Honoria, Bosque Nacional de Iparia, a lo largo del Río Pachitea cerca del campamento Miel de Abeja, 300–400 m, 5 May 1967, *Schunke-Vigo 925* (F, NY, US). JUNIN: Schunke Hacienda, above San Ramón, 1,400–1,700 m, 8–12 June 1929, *Killip 24714* (F, NY, US). LORETO: along Río Amazonas, S of Iquitos, 18 Aug. 1972, *Croat 19309* (F, GH, MO, NY); Maynas, Moena Cano between Iquitos and Río Itaya, 7 Jan. 1976, *Gentry 15654* (F, MO, NY); Balsapuerto, 220 m, Apr. 1933, *Klug 3015* (A, F, GH, MO, NY, US); Coronel Portillo, Bosque Nacional de Iparia, a lo largo del Río Ucayali cerca del pueblo de Iparia, 18 Aug. 1968, *Schunke-Vigo 2617* (F, GH, MO). MADRE DE DIOS: Tambopata, Tambopata Nature Reserve, ca. 30 air km SSW Puerto Maldonado at effluence Río La Torre/Río Tambopata (SE bank), 12°49′S, 69°17′W, 260 m, 17 May 1980, *Barbour 5332* (F, MO,

NY). SAN MARTIN: Juan Jui Alto Río Huallaga, 400 m, Oct. 1934, *Klug 3919* (F, GH, MO, NY, US); near Boquerón, Boquerón Pass, 92 km from Tingo María on highway to Pucallpa, 400 m, 16 Dec. 1949–5 Jan. 1950, *Allard 22074* (US); Mariscal Caceres, Uchiza, E of Puente del Río Uchiza, 400 m, 25 July 1974, *Schunke-Vigo 7767* (MO, US); Marsical Caceres, Tocache Nuevo, Puerto Pizana, Río Huallaga, 350 m, 4 June 1974, *Schunke-Vigo 6898* (MO, US). TUMBES: Zarumilla, Bosque Nacional de Tumbes, cerca de Campo Verde, 600–800 m, 17 Dec. 1967, *Simpson 380* (F, NY). UCAYALI: Bosque von Humboldt, entrance to Carretera Marginal, km 88 of Pucallpa–Tingo María Road, 75°02′W, 08°45′S, 220 m, 14 June 1987, *Gentry 58344* (F, MO). BRAZIL. AMAZONAS: Manariao, basin of Rio Juruá, 27 May 1933, *Krukoff 4589* (A, F, MO, NY, US); basin of Rio Juruá, near mouth of Rio Embira (tributary of Rio Tarauaca), 7°30′S, 70°15′W, 1 July 1933, *Krukoff 5150* (A, F, MO, NY, US).

**5. Malvaviscus williamsii** Ulbr., Notizbl. Bot. Gart. Berlin-Dahlem 11: 545. 1932. *Malvaviscus arboreus* var. *williamsii* (Ulbr.) Schery, Ann. Missouri Bot. Gard. 29: 226. 1942. TYPE: Peru. Loreto: Lower Río Nanay, forest between Río Nanay and Río Napo, 6 June 1929, *L. Williams 706* (holotype, B destroyed?; isotype, F not located). Ulbrich cited only two specimens, one at B the other at F, neither of which we could locate. From the description and location there is little doubt as to the identity of the material concerned. In lieu of extant types we have proposed the following: NEOTYPE: Peru. Loreto: Maynas, "trail between Río Amazonas above Indiana and Mazan (Río Napo) between Mazan and halfway," mature upland rainforest over clay, 100–130 m, 5 July 1971, *Sidney McDaniel 15218* (neotype, MO; isoneotype, F). Figure 4.

Erect or clambering (lianalike) shrub to 7 m high, stems densely and evenly pubescent with short hairs (the felt ca. 0.2 mm high). Leaves mostly 10–30 cm long, 6–22 cm wide; petioles 3–16 cm long, pubescent like the stems; blades mostly cordate, rarely subcordate, the margins irregularly dentate to nearly entire. Flowers mostly axillary and single along the upper stems, erect or occasionally pendulous; corollas pink to bright carmine, 48–70 mm long, at least some of them lobed, the apical portion usually flaring at anthesis and the staminal column usually exserted for 10–30 mm. Calyces 18–30 mm long in fruit, usually densely pubescent with long, stellate, yellowish hairs, the associated bracts 5 or 10, 10–18 mm long, 4–8 mm wide, broadly elliptical-ovate, widest at or near the middle, sparsely stellate pubescent, the margins mostly strongly imbricate. Fruits red (white), 8 mm high, 15–30 mm diam., fleshy at maturity.

*Distribution (Fig. 3).* Northwestern South America, along the Pacific Coast tributaries of western Colombia, and also in a restricted area on the eastern slopes of the Andes, along the Napo River in Peru; flowering all seasons.

*Diagnosis and relationships. Malvaviscus williamsii*, because of the very broad imbricate bracts (Fig. 4), is readily distinguished from the seemingly sympatric *M. concinnus*. The former, however, occurs mostly along the Pacific Coast tributaries, although the type is from the eastern slopes of the Andes, mainly along the Napo River in Peru (Fig. 3). Material from the latter region is essentially indistinguishable from that of the Pacific coastal region. Populations of *M. concinnus* are not known to occur with or especially close to *M. williamsii*, nor does the principal character (bract shape), which distinguishes between the two, irreverentially crop up hither and yon, as occurs with most other "diagnostic" characters in the genus *Malvaviscus*. Most specimens of *M. concinnus* have linear or linear-lanceolate bracts (mostly 1–3 mm wide), which are broadest at or near the base; occasional specimens, however, have somewhat broader bracts (3–5 mm) and may be said to approach the character state found at the type locality of *M. williamsii*. Because of this, some workers might prefer to accord the taxon only varietal rank, as was done by Schery (1942). But among the species of *Malvaviscus*, it is as distinct and probably more so than *M. achanioides* and *M. penduliflorus*, which are retained. In short, our specific assessments are consistent with our evaluation and treatment of the *M. arboreus* complex of North America.

*Additional specimens examined.* COLOMBIA. ANTIOQUIA: Mpio. de Turbo, carretera Tapon del Darien, 10–20 m, *Brand & Narváez 620* (MO, HUA); Mpio. Chigorodo, ca. 15 km W of Chigorodo, ca. 100 m, 14 Mar. 1962, *Feddema 1893* (NY); Mpio. Chigorodo, Vereda Malagon, ca. 20 m, 11 Feb. 1986, *Renteria 4505* (MO); Mpio. Uraba, ca. al Río Chado, 70–90 m, Feb. 1950, *Uribe 2024* (US—2 sheets). CHOCO: Mpio. de Río Sucio, orillas del Río Truando, entre la confluencia de los Ríos Chintado y Salado, *Romero-Castaneda 6121* (MO); orillas del Río Truando, 24 Oct. 1956, *Romero-Castaneda 4674* (MO); near Madurex Logging Camp above Teresita, below rapids on Río Truando, 7–8 Feb. 1967, *Duke 9992* (MO); area of Baudo on Río Baudo, ca. 5 m, 3 Feb. 1967, *Fuchs et al. 21725* (MO, US); area of Baudo, 11 Feb.–29 Mar. 1967, *Fuchs & Zanella 22225* (US—2 sheets); 8–10 km E of Tutunendo, 150

FIGURE 4. *Malvaviscus williamsii* (*Feddema 1893*, US).

m, 14 June 1982, *Gentry & Brand 36872* (MO); between Bolívar and Quibdo, 290 m, 8 Nov. 1983, *Juncosa 1338* (MO). PERU. LORETO: Gamitanacocha, Río Mazan, 100–125 m, 20 Feb. 1935, *Schunke-Vigo 293* (A, F, NY, US); Maynas, Río Momon hacia arriba caserios de San Francisco, 130 m, 8 Mar. 1978, *Díaz & Jaramillo 129* (F, MO). NARIÑO: between Tumaco and El Diviso, along Río Mojada, 150 m, 8 Jan. 1956, *Vogel 32* (US).

## EXCLUDED NAMES

*Malvaviscus palmatus* Ulbr., Verh. Bot. Vereins Prov. Brandenburg 1908: 89. 1909. TYPE: Brazil. Minas Gerais: "am oberen [Rio] Juruá," 25 Apr. 1901, *E. Ule 5443* (holotype, B destroyed?; isotype, MG).

Schery (1942), not having examined type material, accepted this species in *Malvaviscus* with reservation, noting, "from description only, it is difficult to say with surety that this species may not belong in the genus *Pavonia*; yet Ulbrich's description of the fruit and his excellent illustration of the type specimen indicate that this plant probably is a *Malvaviscus*. On the other hand, the original description does not state that the petals are auriculate, from which the inference is that the plant may be *Pavonia*." Examination of the type shows the fruit, which was described by Ulbrich as "niger baccatus," to be rather rigidly, or not clearly, bacculate, having five well-defined fused carpels each with a small, smooth, rounded ridge extending down its length, the whole appearing brownish red. In short, the fruit is *not* clearly black and fleshy as described, although this might have been so in living material; there is no indication that Ulbrich observed fresh fruits, and our observations leave the matter moot. Regardless, dissection of the corolla did not reveal any clearly defined auricles on the petals, and because of this and the seeming absence of stellate pubescence and the markedly palmately lobed leaves, we here transfer the species to *Pavonia*.

**Pavonia palmata** (Ulbr.) B. Turner & M. Mendenhall, comb. nov. *Malvaviscus palmatus* Ulbr., Verh. Bot. Vereins Prov. Brandenburg 1908: 89. 1909. TYPE: Brazil. Minas Gerais: "am oberen [Rio] Juruá," 25 Apr. 1901, *E. Ule 5443* (holotype, B destroyed?; isotype, MG).

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# THE RISE AND FALL OF *PSEUDOLUDOVIA ANDREANA* (CYCLANTHACEAE)[1]

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ABSTRACT

*Pseudoludovia andreana*, described in a monotypic genus, is based on a mixed collection. The element here selected as lectotype is conspecific with *Sphaeradenia laucheana*. *P. andreana* is reduced to a synonym of *S. laucheana*, and *Pseudoludovia* is placed into synonymy under *Sphaeradenia*. *Sphaeradenia laucheana* is neotypified.

In the most recent monograph of the Cyclanthaceae, Harling (1958) recognized 11 genera. Since then, two additional genera have been described, *Chorigyne* (Eriksson, 1989) and *Dianthoveus* (Hammel & Wilder, 1989). The existence of the monotypic genus *Pseudoludovia* Harling has been questioned lately, however, and the genus has not been accounted for in recent investigations of the Cyclanthaceae (Wilder, 1978, 1981; Eriksson, 1989; Hammel & Wilder, 1989).

An André collection (no. 2298) from rather high altitudes in central Colombia, with a fertile specimen deposited at K and a sterile duplicate at NY (Harling, 1958), gave rise to *Pseudoludovia andreana* Harling. A sterile specimen from southern Colombia was also cited in the original description. The genus combined characteristics of both *Ludovia* and *Sphaeradenia*. The leaves of these collections are entire, the habit is climbing as in *Ludovia*, and the young infructescence has united pistillate flowers with one apical placenta, concrescent styles, well-developed tepals, and asymmetrical staminate flowers as in *Sphaeradenia*. Superficially, the vegetative and fruiting parts of the material in K seem to be connected (Fig. 1).

In 1974 in southern Colombia, Wilder and Hernandez collected live, sterile material of a species with entire leaves, which resembled those described for *Pseudoludovia andreana* (Wilder, 1978). In cultivation, part of this material developed inflorescences that clearly showed it to belong to the genus *Ludovia*. At that time Wilder (1978) questioned the existence of *Pseudoludovia*, due to the similarity of the leaves. Furthermore, he suggested that if *Pseudoludovia andreana* was based on a mixed collection, the infructescence should be selected as type material. Consequently, he described his material as the new species *Ludovia bierhorstii* G. Wilder. Later he had the characteristics of the type of *P. andreana* in K described to him, which supported his earlier view (Wilder, 1981).

During a visit to the herbarium at Kew, I examined the type of *Pseudoludovia andreana* and concluded that this taxon is based on a mixed collection. This conclusion is based on the following: (1) The leaf is very similar to those of the later described *Ludovia bierhorstii*. (2) The young fruiting spadix has the same morphology as those of *Sphaeradenia laucheana* (Mast.) Harling. (3) The infructescence is not connected to the vegetative parts, but has been mounted to simulate connection. The fractures of the pieces do not match, and the epidermal cells differ somewhat between them. (4) The part interpreted by Harling as the lower part of the peduncle (Fig. 1, below arrow) is most certainly a stem fragment, which would be consistent with a lianalike habit. This being a peduncle, the plant would have a terminal inflorescence. This condition is unknown in the *Sphaeradenia* group, to which *Sphaeradenia* and *Ludovia* belong and to which *Pseudoludovia* was assigned. (5) No further fertile material of *Pseudoludovia* has ever been found, although it has been looked for. All fertile collections with leaves like those described for *P. andreana* have turned out to be *L. bierhorstii*. Furthermore, *S. laucheana* has recently been collected in the vicinity of the type locality of *P. andreana*. (6) A line on the label of *André 2298* reads "fol. . . . ad apic. bifid." [leaves . . . towards apex bifid], which is not the case with the leaf on the sheet. However, the statement would fit a *Sphaeradenia* species.

I think it is most probable that the mixture has been made after the material had been sent from

[1] I thank Lennart Andersson for reading the manuscript and suggesting improvements, and Gunnar Harling and George Wilder for sharing their points of view on the subject.

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South America, since *L. bierhorstii* is known only from the lowlands of southern Colombia and northern Ecuador and not from the area stated on the label.

According to the *International Code of Botanical Nomenclature* (ICBN) articles 7.4 and 9.2 (Greuter et al., 1988), one of the elements of this mixed collection must be selected as lectotype. Harling's description is based on both elements and gives no indication to which the name should be attached. Wilder has typified the taxon to which the leaf belongs with other material (Wilder, 1978), and his name *Ludovia bierhorstii* has been accepted and used. Designating the leaf as type would reduce this name to a synonym. I therefore select the infructescence of *André 2298* (K) as lectotype for *Pseudoludovia andreana*. This is in accordance with ICBN recommendation 7B.5 (Greuter et al., 1988). Accordingly, the specimen labeled as *André 2298* at NY, consisting of only vegetative parts, should not be regarded as a duplicate of the type collection.

*Pseudoludovia andreana*, typified with the infructescence of *André 2298* (K), clearly belongs to the earlier described genus *Sphaeradenia* (Harling, 1954). The well-developed adaxial perianth lobes of the staminate flowers, the slightly elongate anthers without secretion globule, the free and cuspidate tepals that are rather thick at base and have an apical glandule, and the stigmas that are lanceolate seen from above and do not surpass the tepals in height fall well within the variation range of, and show that it is conspecific with, *Sphaeradenia laucheana*. The latter name is earlier and has priority (ICBN 57.1, Greuter et al., 1988). Consequently I reduce *P. andreana* to a synonym of *S. laucheana*, leaving the genus *Pseudoludovia* to fall into synonymy under *Sphaeradenia*.

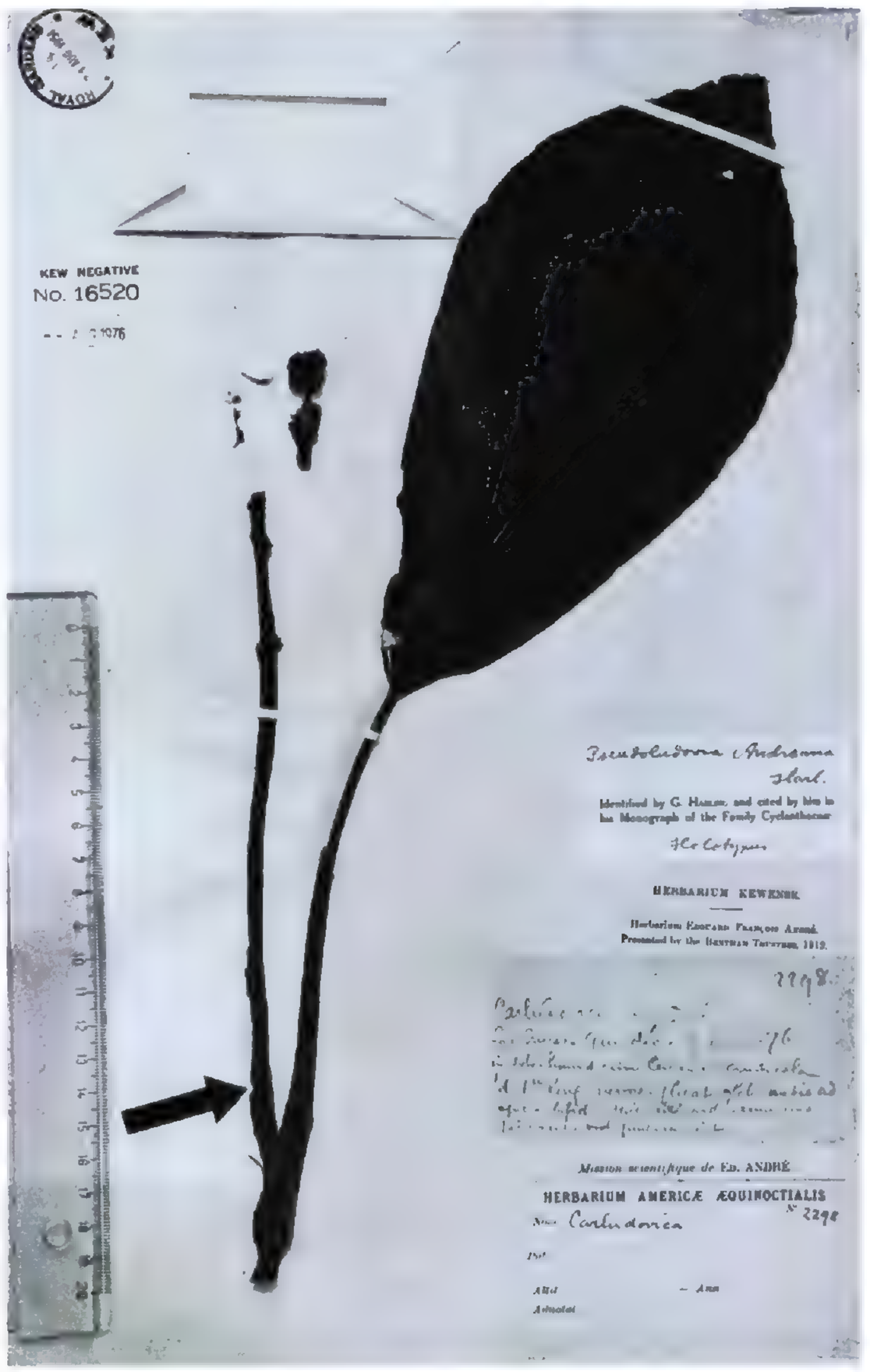


FIGURE 1. The mixed type specimen of *Pseudoludovia andreana* in K. The arrow indicates where the different parts have been mounted together.

**Sphaeradenia laucheana** (Mast.) Harling, Acta Horti Berg. 17: 3. 1954. *Salmia laucheana* Hort. Sander. ex Mast., Gard. Chron., ser. 3, 13: 442. 1893. *Carludovica laucheana* (Mast.) Hook. fil., Curtis's Bot. Mag., ser. 3, vol. 55, tab. 7683. 1899. TYPE: *27 May 1897, Hort. Kew s.n.* (neotype, selected here, K).

*Pseudoludovia andreana* Harling, Acta Horti Berg. 18: 340. 1958. TYPE: Colombia. Tolima, Quindío or Risaralda: Las Cruces, Quindío, 9 Mar. 1876, *André 2298* (infructescence) (lectotype, selected here, K).

*Sphaeradenia laucheana* (Mast.) Harling was imported from Antioquia, Colombia, by Sander & Co. of St. Albans (Hooker, 1899) and was presented at the Ghent exhibition in Belgium in 1893. It did not receive any prize, however, as did the cyclanth *Ludovia lancifolia* Brongn. *Gardeners' Chronicle* reported on the exhibition and included an unsigned description of this plant under the name *Salmia laucheana* Hort. Sander (Masters, 1893). This description must be ascribed to M. T. Masters, the editor of the magazine (Stafleu & Cowan, 1981). The beginning of Masters's description reads "Salmia laucheana, Hort. Sander— A cyclanth of the genus Carludovica . . ." According to ICBN 34.2 (Greuter et al., 1988), the assignment to *Carludovica* does not invalidate the name *Salmia laucheana*.

A clone of this plant was received by Kew in 1895; it flowered for the first time in May 1897, when a specimen was pressed. Hooker (1899) redescribed this cultivated material as *Carludovica laucheana* and provided an excellent illustration. He also cited *Salmia laucheana* from *Gardeners' Chronicle*.

Harling (1954) transferred *C. laucheana* to the new genus *Sphaeradenia*. As basionym he cited the name from Hooker's description, regarding *Salmia laucheana* as a "nomen seminudum" (Harling, 1958). However, the description in *Gardeners' Chronicle* is rather exhaustive with respect to vegetative structures, and the name is thus validly published. Harling's incorrect reference to the author of the basionym does not invalidate the combination made by him; it should be regarded as a bibliographic error (ICBN 33.2, Greuter et al., 1988).

There is no original material of *S. laucheana*, and, accordingly, a neotype must be selected. Harling accredited Hooker with the basionym, and therefore he incorrectly regarded the pressed specimen, *Hort. Kew s.n., 27 May 1897* (K), as the holotype. However, because this specimen was prepared from a clone of the original material, I select it as neotype for *Sphaeradenia laucheana*.

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# CHROMOSOME CYTOLOGY IN TROPICAL AFRICAN *GLADIOLUS* (IRIDACEAE)[1]

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## Abstract

Original chromosome counts for 16 species of tropical African *Gladiolus*, 5 southern African, and 3 Eurasian species, 17 of these not before examined, confirm that $x = 15$ is probably the ancestral basic number for the genus. Until now, $x = 15$ has been the only recorded base number in *Gladiolus*, but several tropical African species have been found to depart from this pattern, the only known examples of dysploidy in the genus. In subgenus *Gladiolus*, *G. atropurpureus* has $x = 12$ ($2n = 24 + 0$–$5$B, 36); *G. serapiflorus*, *G. gregarius*, and *G. pseudospicatus* have $x = 11$ ($2n = 22$); *G. unguiculatus* has $x = 13$ ($2n = 26 + 0$–$2$B, also possibly $2n = 24$); and *G. actinomorphanthus* has $2n = 28$. Because on morphological grounds most of these species do not seem to be immediately related, we suggest that dysploid reduction in tropical African *Gladiolus* may have occurred in four separate lineages. Results confirm polyploidy in *G. dalenii*, $2n = 60$ and 90, and the three Eurasian species examined. The first count for the Malawian *G. bellus*, $2n = 60$, indicates polyploidy in only one more tropical African species of *Gladiolus*. Counts of $2n = 39$ in two populations of *G. decoratus* suggest triploidy based on $x = 13$, making this one more possible example of dysploidy for the genus. Although the chromosomes of *Gladiolus* are relatively small, some karyotypic details provide additional data relating to species relationships. Measurements of total chromosome length show that irrespective of base number, most of the diploid species have a comparable amount of chromosome material. Two species, *G. melleri* ($2n = 30$) and *G. decoratus* ($2n = 39$), however, have significantly higher amounts of chromosome material, ca. 33–40% above expected levels, a condition possibly related to their characteristic rapid growth and flowering early in the growing season.

Ever since the first chromosome counts (Vilmorin & Simonet, 1927; Ernst-Schwarzenbach, 1931; Bamford, 1935) were made in *Gladiolus*, the largest and most taxonomically complex genus of Iridaceae subfamily Ixioideae (Goldblatt, 1991), $x = 15$ has been considered the probable ancestral base number for the genus (Goldblatt, 1971). Except for the occasional occurrence of B chromosomes, the several Eurasian, southern African, and Madagascan species counted all have diploid numbers based on $x = 15$ and the only significant cytological variation reported in *Gladiolus* has been polyploidy. Eurasian species are consistently polyploid (van Raamsdonk & de Vries, 1989) while most southern African and all Madagascan species examined are diploid. Until now, only two endemic tropical African species have been studied cytologically (Table 1) and these have corresponded to the Afro-Madagascan pattern in being diploid, $2n = 30$. A third, *G. dalenii*, which also occurs in Arabia, South Africa, and Madagascar, is polyploid in Africa, $2n = 45$, 60, 75, and 90. Counts here for 16 tropical species of *Gladiolus*, 12 never before counted, at least for tropical Africa, and an additional five southern African species, confirm that while $x = 15$ is the probable ancestral base number, important variation occurs in some tropical species. Descending dysploidy, probably in four separate lineages, has led to the establishment of secondary base numbers, $x = 14$, 13, 12, and 11. Polyploidy is confirmed in *G. dalenii* in tropical Africa (the species is diploid in Madagascar). One more tropical species, *G. bellus*, appears to be polyploid. *Gladiolus*, a genus of some 215–220 species, remains poorly sampled cytologically, and in view of the variation recorded here, needs to be investigated in more detail.

## Materials and Methods

Seeds or corms of wild collected species (Table 1) were sprouted in the greenhouse, and emergent leaf and root tips were harvested for analysis of mitosis in one of two ways. For rapid determination

TABLE 1. Chromosome numbers in sub-Saharan African and Madagascan *Gladiolus*. For comparative purposes, some Eurasian species were also examined, but past counts for the area are not reviewed. Original counts are indicated in bold type and provided with collection data; previously published counts are referenced, and nomenclature adjusted to reflect current taxonomy (Lewis et al., 1972; Goldblatt, 1989). Unless otherwise indicated, voucher specimens are housed at MO.

| Species | Diploid number | Collection data or reference |
|---|---|---|
| | | Southeastern and Tropical Africa and Madagascar |
| *G. actinomorphanthus* Duvign. & Bokstael | **28** | Zaire, Shaba, *Schaijes 5090, Schaijes 5152-64* |
| *G. aequinoctialis* Herbert | 30 | Harvey, 1966 (as *Acidanthera*) |
| | **30** | Cameroon, Mt. Bamboutos, *Boussard s.n.* |
| *G. atropurpureus* Baker | **24 + 0–5B** | Zaire, *Schaijes 5178-81, Schaijes 5198*; Malawi, Mt. Malosa, *Goldblatt*, no voucher |
| | **36** | |
| *G. andringitrae* Goldblatt | 30 | Goldblatt, 1989 |
| *G. bellus* C. H. Wright | **60** | Malawi, Mt. Mulanje, *Oliver s.n.* |
| *G. bojeri* (Baker) Goldblatt | 30 | Goldblatt, 1989 |
| *G. callianthus* Marais | 30 | Sharma & Talukdar, 1960; Bannerjee & Sharma, 1971; Goldblatt, 1971; Ohri & Khoshoo, 1985 (all as *Acidanthera bicolor*) |
| *G. crassifolius* Baker | 30 | Bamford, 1935; Goldblatt, 1971 |
| | **30** | Malawi, Mulanje, *Chapman 8364*; Tanzania, Mufindi, *Lovett 3276* |
| | **30(–31)** | Zimbabwe, Nyanga, *Goldblatt 9077* |
| *G. dalenii* Geel | 60 | Vilmorin & Simonet, 1927; Ernst-Schwarzenbach, 1931; Bamford, 1935; Mensinkai, 1939; Ohri & Khoshoo, 1985 (all as *G. primulinus*); Bamford, 1935 (as *G. coccineus*) |
| | 60 | Bamford, 1935 (as *G. platyphyllus*) |
| | 75 | Bamford, 1935 (as *G. quartinianus*) |
| | 75, 90 | Bamford, 1935 (as *G. dracocephalus*) |
| | 75, 90 | Bamford, 1935 (as *G. psittacinus*) |
| | 45, 60, 75 | Goldblatt, 1971 (as *G. natalensis* var. *natalensis* and var. *cooperi*) |
| | 30 | Goldblatt, 1989 |
| | 90 | Paiva & Leitao, 1989 |
| | **60** | Zimbabwe, Nyanga, *Goldblatt s.n.*, no voucher |
| | **90** | Ethiopia, Eritrea, *Ryding 1488* (UPS) |
| *G. decaryi* Goldblatt | 30 + 0–2B | Goldblatt, 1989 |
| | **30** | Madagascar, Talaonaro, *Puff 800803-1/5* |
| *G. decoratus* Baker | **39** | Malawi, Zomba, *Goldblatt 9098*; Luchenza, *la Croix s.n.*, no voucher |
| *G. erectiflorus* Baker | **30** | Malawi, Dedza District, *Goldblatt 9091, Goldblatt 9105*; Zaire, Shaba, *Schaijes 5091* |
| *G. gregarius* Baker | **22** | Central African Republic, *Harris & Fay 2241*; Tanzania, Mufindi, *Lovett 4622*; Tanzania, Njombe, *Spurrier 600*; Zaire, Shaba, *Brooks et al. 165* |
| *G. horombensis* Goldblatt | 30 | Goldblatt, 1989 |
| *G. laxiflorus* Baker | **30** | Tanzania, Mufindi, *Goldblatt et al. 8050* |
| *G. longicollis* var. *platypetalus* (Baker) Oberm. | 30 | Goldblatt, 1971 (as *G. praelongitubus*) |
| *G. luteus* Lam. | 30 | Goldblatt, 1989 |
| *G. melleri* Baker | **30** | Tanzania, Ufipa, *Goldblatt et al. 8135*; Zaire, Shaba, *Schaijes 5113* |
| *G. papilio* Baker hybrid | 75 | Bamford, 1935 |
| *G. pseudospicatus* Cordova | **22** | Zaire, Shaba, *Brooks et al. 199* |
| *G. saundersii* Hook. | 30, 45 | Bamford, 1935 |
| | **30** | South Africa, Naudes Nek, *Batten s.n.* |
| *G. serapiflorus* Goldblatt | **22** | Zaire, Shaba, *Schaijes 5137-42* |

TABLE 1. Continued.

| Species | Diploid number | Collection data or reference |
|---|---|---|
| *G. sericeo-villosus* Hook. | | |
| subsp. *sericeovillosus* | **30** | South Africa, Natal, *Goldblatt & Manning 8430* |
| subsp. *calvatus* (Baker) Goldblatt | **30** | Zimbabwe, Lomagundi, *Goldblatt 9062* |
| *G. varius* Bolus f. | 30 | Goldblatt, 1971 |
| *G. unguiculatus* Baker | **26** | Zaire, Shaba, *Schaijes 5143, 5146, 5148* |
| | **24** | Zaire, Shaba, *Schaijes 5150* |
| | **26 + 2B** | Zaire, Shaba, *Schaijes 5123* |
| | **24, 26** | Zaire, Shaba, *Schaijes 5124* |
| *G. watsonioides* Baker | **30** | Kenya, Mt. Kenya, *Mudge s.n.* |
| *G. zambesiacus* Baker | **30** | Malawi, Mt. Zomba, *Goldblatt 9092, Goldblatt 9099* |
| *G. zimbabweensis* Goldblatt | **30** | Zimbabwe, Nyanga, *Goldblatt 9080* |
| | | Cape species (winter rainfall area of southern Africa) |
| *G. abbreviatus* Andrews | 30 | Goldblatt, 1971; de Vos, 1976 (as *Homoglossum*) |
| *G. alatus* L. | 30 | Bamford, 1935 |
| *G. angustus* L. | 30 | Bamford, 1935; Verryn, 1988 |
| *G. bonaespei* Goldblatt & de Vos | 30 | Goldblatt, 1971; de Vos, 1976 (as *Homoglossum merianellum*) |
| *G. brevifolius* Jacq. | 30 | Bamford, 1935; Goldblatt, 1971 |
| *G. buckerveldii* (L. Bolus) Goldblatt | 30 | Goldblatt, 1971 |
| *G. cardinalis Curt.* | 30 | Ernst-Schwarzenbach, 1931; Brittingham, 1934; Bamford, 1935; Nakajima, 1936 |
| *G. carmineus* C. H. Wright | 30 | Bamford, 1935 |
| *G. carneus* Delaroche | 30 | Bamford, 1935 (as *G. blandus, G. pappei,* and *G. callistus*); Verryn, 1988 |
| *G. caryophyllaceus* (Burm. f.) Poiret | 30 | Bamford, 1935 (as *G. hirsutus*) |
| *G. ceresianus* L. Bolus | 30 | Goldblatt, 1971 |
| *G. cunonius* (L.) Gaertn. | 30 | Goldblatt, 1971 (as *Anomalesia cunonia*) |
| *G. debilis* Ker | 30 | Bamford, 1935 |
| *G. equitans* Thunb. | 30 | Bamford, 1941 (as *G. namaquensis*) |
| *G. floribundus* Jacq. | 30 | Verryn, 1988 |
| *G. gracilis* Jacq. | 30 | Bamford, 1935 |
| *G. gueinzii* Kunze | 30 | Goldblatt, 1971 |
| | **30** | South Africa, eastern Cape, *Goldblatt 9052* |
| *G. huttonii* (N. E. Br.) Goldblatt & de Vos | 30 | de Vos, 1976 (as *Homoglossum*) |
| *G. lapeirousioides* Goldblatt | 30 | Goldblatt, 1974 |
| *G. leptosiphon* Bolus f. | **60** | South Africa, Cape, Cockscomb, *Bongers s.n.* (NBG) |
| *G. liliaceus* Houtt. | 30 | Bamford, 1935 (as *G. grandis*) |
| *G. maculatus* Sweet | 30 | Bamford, 1941 |
| *G. martleyi* L. Bolus | 30 | Bamford, 1941 |
| *G. odoratus* L. Bolus | 30 | Bamford, 1935 |
| *G. oppositiflorus* Herbert | 30 | Bamford, 1935 |
| | 46 | Ernst-Schwarzenbach, 1931 |
| *G. orchidiflorus* Andrews | 45 | Bamford, 1935 |
| *G. permeabilis* Delaroche | | |
| subsp. *permeabilis* | 30 | Bamford, 1935 |
| subsp. *edulis* (Burch. ex Ker) Oberm. | 30 | Nordenstam, 1969; Goldblatt, 1971 (as *G. edulis*) |

TABLE 1. Continued.

| Species | Diploid number | Collection data or reference |
|---|---|---|
| *G. pritzellii* Diels | 30 | Goldblatt, 1971 |
| *G. priori* N. E. Br. | 30 | Goldblatt, 1971 (as *Homoglossum*) |
| *G. punctulatus* Schrank | 30 | Bamford, 1935 (as *G. villosus* and *G. hirsutus*) |
| *G. quadrangulus* Delaroche | 30 | Verryn, 1988 |
| | **30** | South Africa, Cape Flats, *Goldblatt 525* (BOL) |
| *G. recurvus* L. | 30 | Bamford, 1935 |
| *G. saccatus* (Klatt) Goldblatt & de Vos | 30 | Goldblatt, 1974 (as *Anomalesia*) |
| *G. scullyi* Baker | 45 | Bamford, 1935 (as *G. formosus*) |
| *G. sempervirens* G. Lewis | 30 | Bamford, 1935 (as *G. splendens*) |
| *G. tenellus* Jacq. | 30 | Bamford, 1935 (as *G. trichonemifolius*) |
| *G. teretifolius* Goldblatt & de Vos | 30 | de Vos, 1976 (as *Homoglossum muirii*) |
| *G. tristis* L. | 30 | Ernst-Schwarzenbach, 1931; Brittingham, 1934; Bamford, 1935; Mensinkai, 1939; Ohri & Khoshoo, 1985 |
| *G. undulatus* L. | 30 | Bamford, 1935; Ernst-Schwarzenbach, 1931 (also as *G. cuspidatus*); Goldblatt, 1971; Verryn, 1988 |
| *G. uysiae* L. Bolus ex G. Lewis | **30** | South Africa, Cape, Bokkeveld Escarpment, *Goldblatt 4984* |
| *G. watermeyeri* L. Bolus | 30 | Bamford, 1941 |
| *G. watsonius* Thunb. | 30[1] | Bamford, 1941; Goldblatt, 1971; de Vos, 1976 (as *Homoglossum*) |
| *G. atroviolaceus* Boiss. | **60** | Iran, Qushi Pass, *Goldblatt 850* |
| *G. byzantinus* L. | **90** | Morocco, cult. Missouri Botanical Garden, *Goldblatt s.n.* |
| *G. kotschyanus* Boiss. | **60** | Iran, Baneh, *Goldblatt 901* |

[1] Counts of $2n = 66$ for *G. watsonius* (as *Homoglossum*) by Sharma & Talukdar (1960) are almost certainly based on misidentified plants.

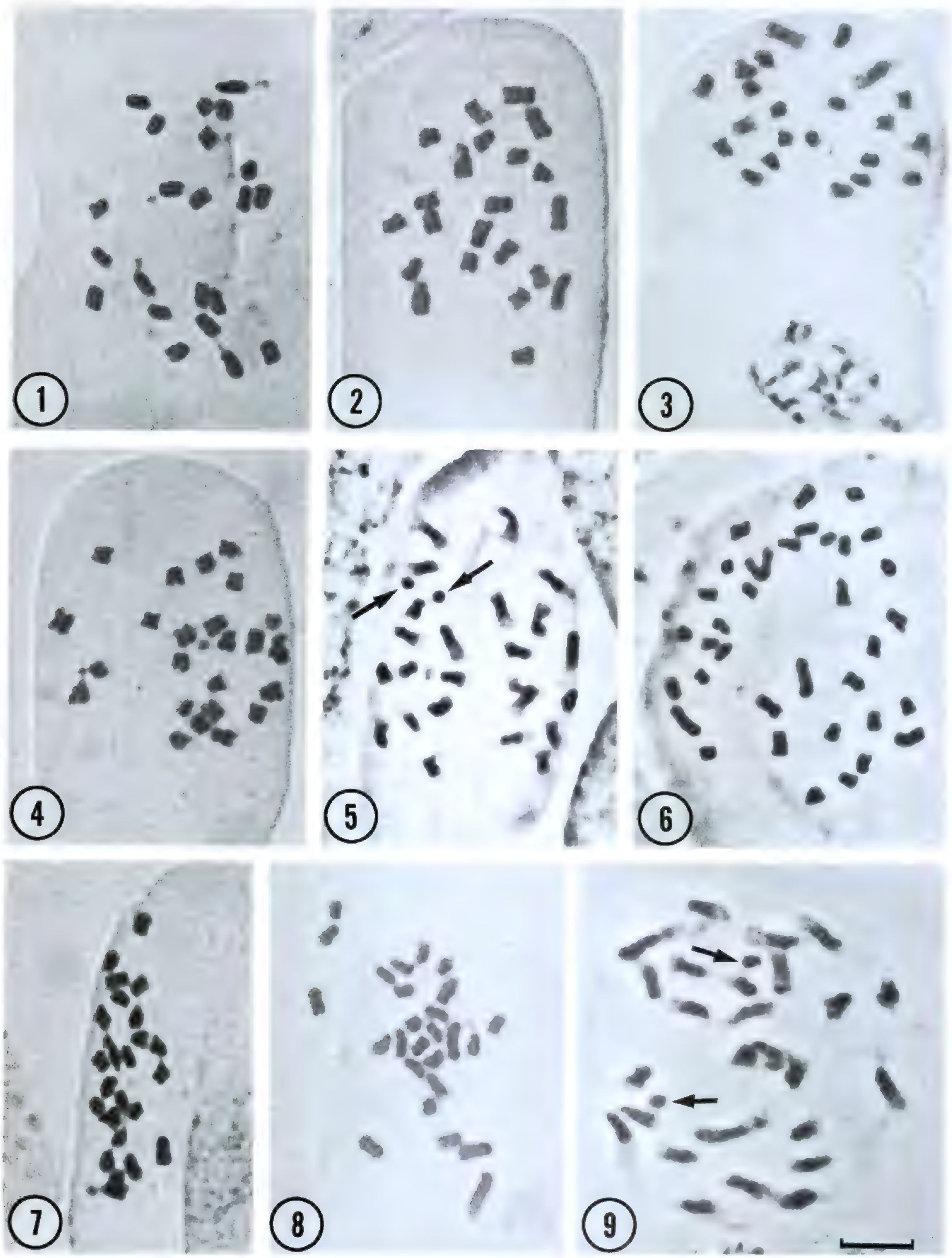
of chromosome number, root tips were pretreated in saturated aqueous m-bromonaphthalene for 4 hours at room temperature, then fixed in 3:1 absolute ethanol-glacial acetic acid for 5 minutes. After hydrolysis in 10% HCl at 60°C for 6 minutes, tips were squashed in FLP orcein (Jackson, 1973). For more critical analysis, leaf and root tips were pretreated in 0.002 M aqueous 8-hydroxyquinoline for 4–5 hours at room temperature, then fixed in modified Carnoy's solution (absolute ethanol-glacial acetic acid-chloroform 6:3:1) at 8°C for about 24 hours. Both root and leaf tips were stained in Feulgen reagent and squashed in 1% aceto-orcein. Photographed preparations were all made using the latter technique.

## OBSERVATIONS

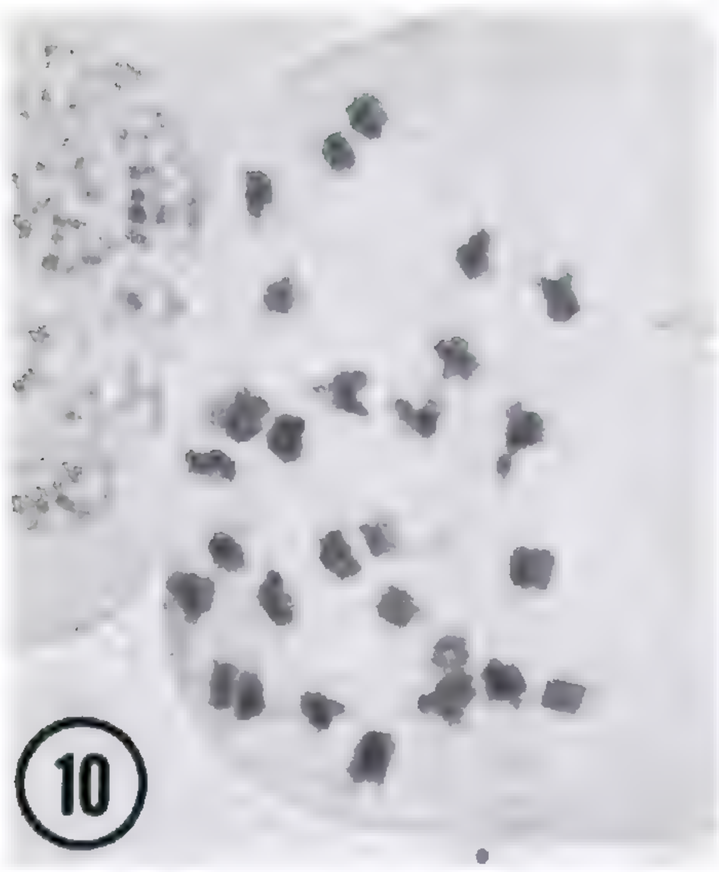
Chromosomes of *Gladiolus* are relatively small, 0.7–2.9 μm (Figs. 1–21), and diploid numbers are based on $x = 15$ in the majority of species examined (Table 1). Several tropical African species differ in base number. The common tropical African species *G. gregarius* has $2n = 22$, based on counts from four populations as far apart as Central African Republic, southern Zaire, and Tanzania; closely related *G. pseudospicatus*, centered in southern Zaire and most common on soils with high concentrations of heavy metals, also has $2n = 22$ (Figs. 1, 2). *Gladiolus serapiflorus* has $2n = 22$, based on several counts from a single population from Zaire (Fig. 3). The widespread *G. atropurpureus* appears to have $x = 12$: two populations from Zaire have $2n = 24$, sometimes with B chromosomes ranging in number from 1 to 5 (Figs. 4, 5); and three individuals in a population from Malawi are triploid, $2n = 36$ (Fig. 6).

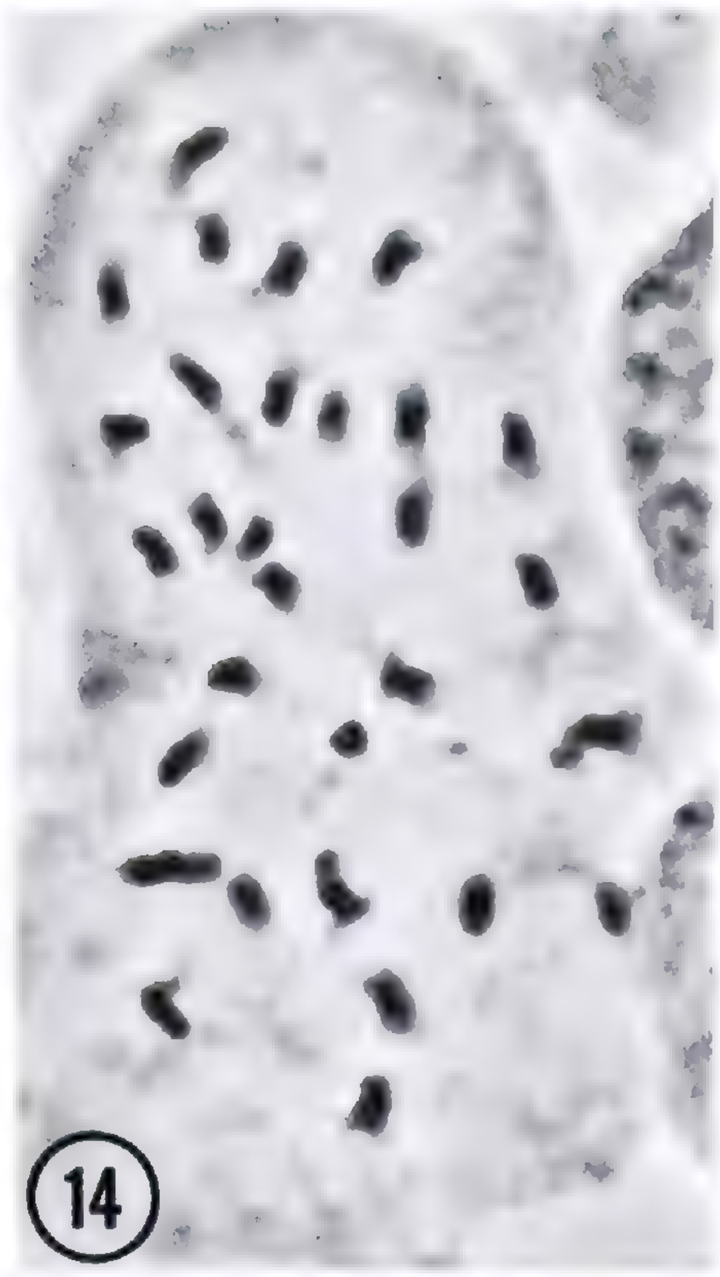
The widespread and common *Gladiolus unguiculatus* has proven cytologically puzzling. While most plants sampled from two populations in southwestern Zaire have $2n = 26$ (or $2n = 26 + 2B$), some individuals have $2n = 24$ (Figs. 7–9). The Zairean endemic, *G. actinomorphanthus*, has $2n = 28$ (Fig. 10) in two populations examined.

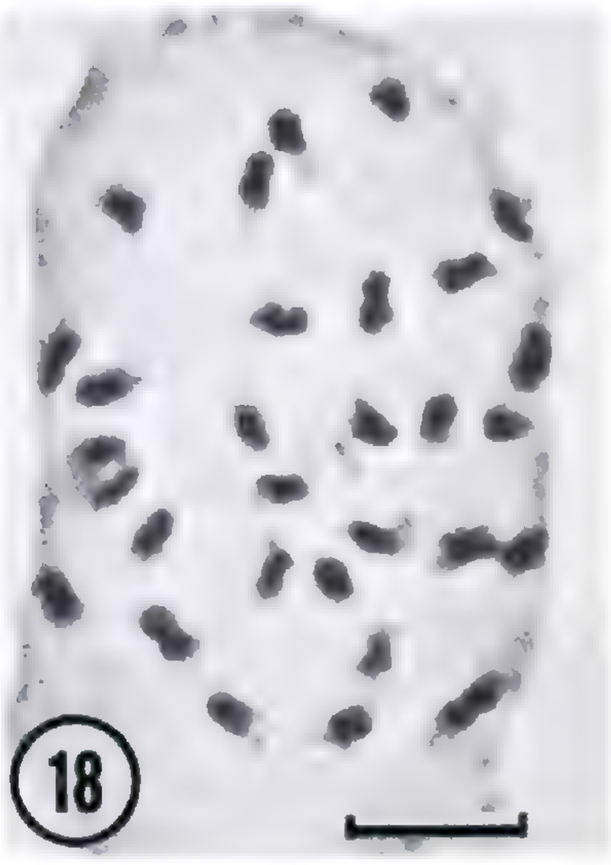
Karyotypes of most species comprise metacentric to submetacentric chromosomes (symmetrical



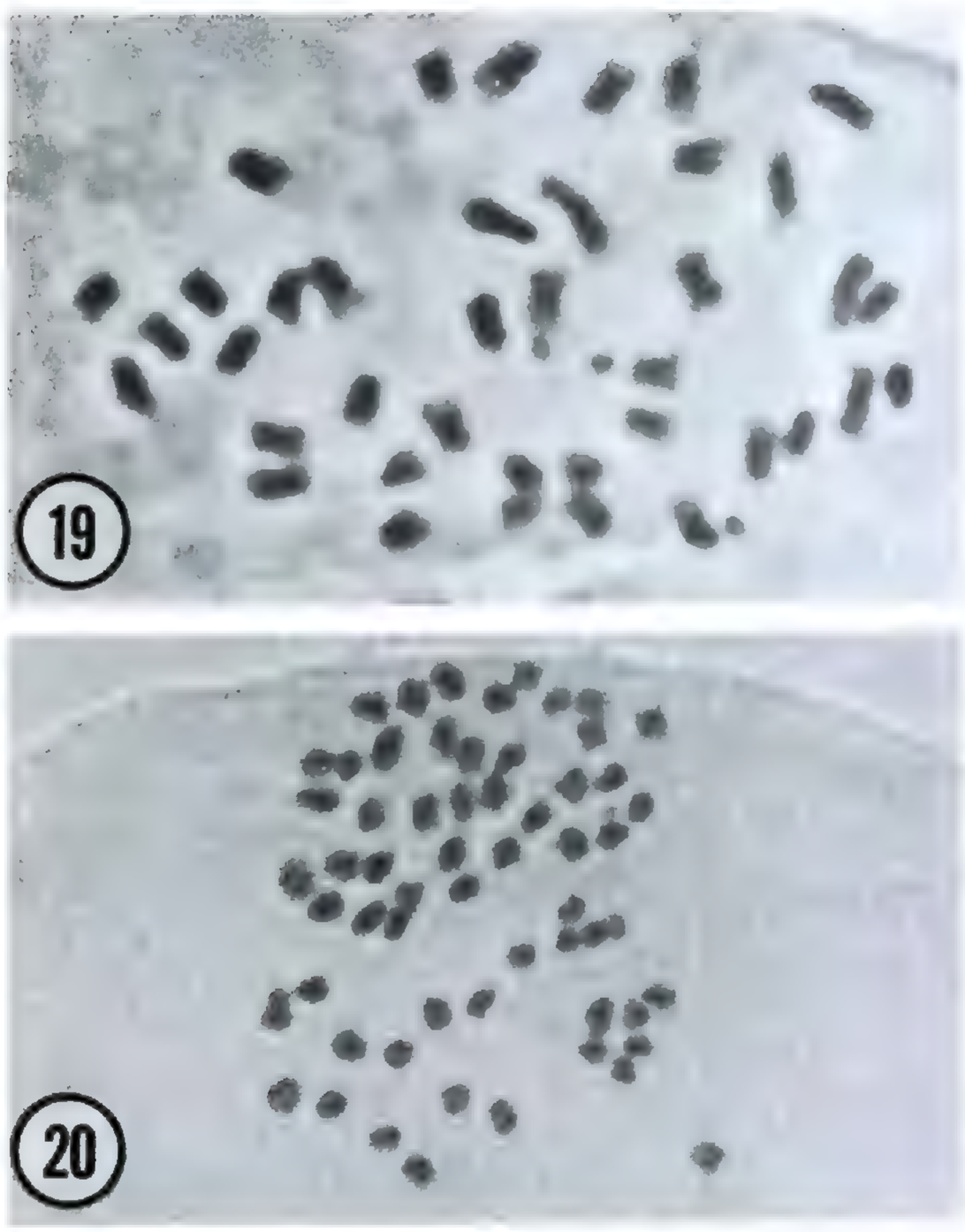

FIGURES 1–9. Mitotic metaphase in *Gladiolus*.—1. *G. pseudospicatus* ($2n = 22$).—2. *G. gregarius* ($2n = 22$).—3. *G. serapiflorus* ($2n = 22$).—4. *G. atropurpureus* ($2n = 24$).—5. *G. atropurpureus* ($2n = 24 + 2B$).—6. *G. atropurpureus* ($2n = 39$).—7. *G. unguiculatus* ($2n = 24$).—8. *G. unguiculatus* ($2n = 26$).—9. *G. unguiculatus* ($2n = 26 + 2B$). B chromsomes are indicated by the arrows. Scale bar = 5 μm.








FIGURES 10–18. Mitotic metaphase in *Gladiolus*. 10. *G. actinomorphanthus* ($2n = 28$).—11. *G. crassifolius* ($2n = 30$).—12. *G. crassifolius* ($2n = 31$).—13. *G. decaryi* ($2n = 30$).—14. *G. zambesiacus* ($2n = 30$).—15. *G. zimbabweensis* ($2n = 30$).—16. *G. melleri* ($2n = 30$).—17. *G. gueinzii* ($2n = 30$).—18. *G. sericeovillosus* subsp. *calvatus* ($2n = 30$). Scale bar = 5 μm.



FIGURES 19–21. Mitotic metaphase in *Gladiolus*.—19. *G. decoratus* ($2n = 39$).—20. *G. bellus* ($2n = 60$).—21. *G. byzantinus* ($2n = 90$). Scale bar = 5 μm.

in arm ratio) of fairly uniform size. All chromosomes have a large heterochromatic segment that stains darkly at early prophase. In *Gladiolus gregarius*, *G. pseudospicatus*, and *G. decoratus*, each with the longer chromosomes 2.1–2.7 μm long, thus exceeding the average, the size range is continuous. However, bimodal karyotypes with one or two conspicuously longer chromosome pairs 2.4–2.9 μm long, characterize *G. atropurpureus*, *G. serapiflorus*, and the $2n = 26$ cytotypes of *G. unguiculatus* (Figs. 3–5). The Mediterranean *Gladiolus byzantinus*, $2n = 90$, included in this study for comparative purposes, also has a bimodal karyotype (Fig. 21), but only one pair of longer chromosomes despite its hexaploid karyotype.

Total chromosome length, a comparative measure of genome size, is similar in most of the diploid species (Table 2), irrespective of base number, and most species have between 31.4 and 39.5 μm of chromosome material. This supports our view that dysploidy alone has been responsible for changes in base from $x = 15$ to 11. Two species, *G. melleri* and *G. decoratus*, have significantly higher amounts of chromosome material, 33–40% above expected levels. We suggest that this may be related to their comparatively rapid growth patterns early in the growing season. Both complete their flowering by the end of December, or earlier, and within the first few weeks of the rainy season. Other species with similar growth patterns such as *G. unguiculatus* and *G. atropurpureus* do not have comparably enlarged genomes (Table 2).

There is usually one pair of satellites per chromosome complement in diploid species ($2n = 22$–30). In *G. atropurpureus*, however, there are consistently two pairs of satellites (satellite number in the presumed triploid plants is uncertain). In the population of *G. decoratus* that we examined, also presumably triploid, the karyotype includes three satellite chromosomes.

Polyploidy is reconfirmed for tropical African *Gladiolus dalenii* and for the Eurasian *G. byzantinus*. An Ethiopian population of *G. dalenii* has $2n = 90$, and one from Zimbabwe has $2n = 60$. The Malawian endemic *G. bellus*, not before counted, has $2n = 60$ (Fig. 20) and must be assumed to be a tetraploid species. Counts of $2n = 39$ in *G. decoratus* (Fig. 19), obtained from corms of three individuals of one population from southern Malawi, and from one corm of a second population, suggest triploidy and a base number of $x = 13$ for the species. This awaits confirmation when more material becomes available. Counts for both Asian species examined, *G. kotschyanus* and *G. atroviolaceus*, $2n = 60$, are consistent with polyploidy in other Eurasian species of *Gladiolus*, but the only other count for the latter, $2n = 45$ (van Raamsdonk & de Vries, 1989), is puzzling.

TABLE 2. Total length (μm) of metaphase chromosome complement of selected species of *Gladiolus*, mostly from tropical Africa. Bimodal karyotypes are indicated by X. Figures in parentheses for *G. unguiculatus* refer to voucher numbers in Table 1.

| Taxon | Diploid number $2n$ | Size range μm | Total chromosome length μm | Length of basic set μm | Bimodality |
|---|---|---|---|---|---|
| *G. actinomorphanthus* | 28 | 1.8–0.9 | 34.7 | 17.4 | — |
| *G. atropurpureus* | 24 | 2.3–1.3 | 41.4 | 20.7 | — |
| | 36 | 2.9–1.1 | 56.9 | 18.9 | X |
| *G. bellus* | 60 | 1.4–0.7 | 67.3 | 16.8 | — |
| *G. crassifolius* | 30 | 1.4–0.7 | 31.3 | 15.7 | — |
| *G. decaryi* | 30 | 1.8–0.8 | 34.6 | 17.3 | X |
| *G. decoratus* | 39 | 2.6–1.6 | 77.3 | 26.4 | — |
| *G. gregarius* | 22 | 2.4–1.4 | 37.6 | 18.8 | — |
| *G. gueinzii* | 30 | 2.2–1.0 | 39.5 | 19.8 | — |
| *G. melleri* | 30 | 2.2–1.2 | 48.9 | 24.5 | — |
| *G. pseudospicatus* | 22 | 2.1–1.1 | 34.4 | 17.2 | — |
| *G. serapiflorus* | 22 | 2.5–1.2 | 33.3 | 16.7 | X |
| *G. sericeovillosus* subsp. *calvatus* | 30 | 1.5–0.8 | 31.4 | 15.7 | — |
| *G. unguiculatus* (*5124*) | 26 | 2.4–1.1 | 41.0 | 20.5 | X |
| (*5148*) | 26 | 2.5–1.1 | 39.7 | 19.9 | X |
| (*5150*) | 24 | 2.0–1.0 | 34.0 | 17.0 | — |
| *G. zambesiacus* | 30 | 1.4–0.9 | 32.7 | 16.4 | X |

B chromosomes, reported in *Gladiolus* previously only in the Madagascan *G. decaryi* (Goldblatt, 1989), seem common in *G. atropurpureus* and *G. unguiculatus*. Additional *G. decaryi*, examined here, lacked B chromosomes. As is usual with B chromosomes, they are small, ca. 0.8 μm long, often vary in number within individuals, and can be recognized at prophase by their precocious and uniformly dark staining (Figs. 5, 9). Whether the variation in chromosome number in *G. unguiculatus*, either $2n = 24$ or 26, is also due to the presence of a type of B or supernumerary chromosome has not been established. In plants with $2n = 26$, the number is consistent in several individuals examined, and no precocious staining was noted except when the number exceeded 26, when typical B chromosomes could be identified. We suspect that plants with $2n = 24$ may be hybrids, perhaps with *G. serapiflorus*, $2n = 22$, which grows at the same site. Study material was collected in fruit, and counts were obtained from germinating seeds. This makes it impossible to confirm hybridity in the vouchers, at least until seedlings flower in 3–4 years. Provisionally we assume that *G. unguiculatus*, at least in southern Zaire, is dysploid, normally with $2n = 26$.

We are uncertain whether the additional chromosome in one plant of a Zimbabwean population of *G. crassifolius* is a B chromosome or not, but other individuals examined have a normal complement of $2n = 30$.

## DISCUSSION

Including the original counts in this paper, and after bringing the taxonomy up to date, some 75 species of *Gladiolus* are known cytologically (Table 1). Although this seems substantial, it is less than 35% of the estimated 220 species in the genus (Goldblatt, in prep.). The first chromosome counts made in *Gladiolus* (Vilmorin & Simonet, 1927; Ernst-Schwarzenbach, 1931; Bamford, 1935) established $x = 15$ as the likely ancestral base number for the genus. Although most Cape and eastern southern African species counted were diploid, $2n = 30$, these early studies also suggested that polyploidy was common in *Gladiolus*. Studies by Lewis et al. (1972) and Geerinck (1972) indicate that the several tropical and eastern southern African polyploid species recognized in these early cytological studies are conspecific (Table 1), and the earliest name for the species has been shown to be *G. dalenii* (Hilliard & Burtt, 1979). It is now evident that polyploidy is uncommon in *Gladiolus* outside Eurasia, where species are tetraploid to dodecaploid, except for a puzzling count of $2n = 45$ in *G. atroviolaceus* (van Raamsdonk & de Vries, 1989). Outside Eurasia *Gladiolus* is pre-

dominantly diploid, and dysploidy is more frequent than polyploidy.

The ancestral basic chromosome number in *Gladiolus* is probably $x = 15$, as assumed in the past (Goldblatt, 1971). The species in which dysploidy occurs all seem specialized, although in different ways. Thus none seems a suitable candidate for an ancestral position in the genus in which several broad foliage leaves, branched stems, broadly winged seeds, and a base number of $x = 15$ appear symplesiomorphic (Goldblatt, 1991; in prep.). The species in which dysploidy occurs are all small-flowered and small in stature, both features probably plesiomorphic in *Gladiolus*. Except for *G. actinomorphanthus*, they also all have clawed tepals grooved toward the base and united for a short distance, a probable synapomorphy uniting about half the species of the genus in subgenus *Gladiolus*.

No other characters unite all the dysploid species, and we conclude that except for *G. atropurpureus* and *G. serapiflorus*, which appear closely related, descending dysploidy has occurred independently in four lineages. This conclusion is partly supported by the karyotypes. Those of *G. atropurpureus* and *G. serapiflorus* are bimodal with a single comparatively long chromosome pair. Morphologically, *G. atropurpureus* and *G. serapiflorus* seem united in their very short foliage leaves, often reduced to sheaths with vestigial blades, and coarsely fibrous corm tunics.

*Gladiolus gregarius* and *G. pseudospicatus* have three synapomorphies, two unique in the genus, long imbricate bracts and a short style with short branches, and a third, unbranched stems. *Gladiolus unguiculatus* also has unbranched stems but is remarkable in having flowering and vegetative cycles at different seasons. Lastly, *G. actinomorphanthus*, which seems primitive in having actinomorphic flowers, belongs to an alliance of species adapted to unusual soil conditions that have terete 4-grooved leaves and seeds in which the wings are reduced to vestigial ridges.

Polyploidy has evidently played a minor role in the evolution of *Gladiolus*, except in Eurasia and North Africa where a single polyploid event in the founding population, ancestral to all the species in the region, could account for the pattern here. Polyploidy elsewhere has been sporadic. Except for reports of triploidy in *G. scullyi* and *G. orchidiflorus* (Table 1) that need additional study, only one species in the Cape region, tentatively assigned to *G. leptosiphon*, is polyploid. Excluding *G. dalenii* and *G. bellus*, only two tropical and eastern southern African species have been reported as polyploid, *G. papilio* and *G. saundersii*, and both the latter counts are for so-called hybrids (Bamford, 1935). At least wild *G. saundersii* appears to be diploid. The significance of polyploidy in *G. dalenii* is difficult to gauge. It is one of the most successful species of the genus, and certainly the one with the widest geographical distribution (Goldblatt, 1989; in prep.). It extends from the eastern Cape, South Africa, to Senegal in West Africa and from Madagascar to Ethiopia and Yemen. Perhaps polyploidy has played a role in enabling the species to thrive under the wide range of conditions that occur across its range. The role of humans in its dispersal may also be important. The species is cultivated in West Africa, and as an important medicinal plant it may have been spread over long distances by human agency.

The presumed ancestral basic chromosome number in *Gladiolus*, $x = 15$, is shared in subfamily Ixioideae only with the mono- or ditypic *Radinosiphon* (Goldblatt, 1971), and the two genera are evidently palaeotetraploid. This base number is apomorphic in Ixioideae, and it is the only synapomorphy uniting *Gladiolus* and *Radinosiphon*. Most other genera of Ixioideae have lower base numbers (Goldblatt, 1971), $x = 11$ and 10 being most frequent. Other high base numbers in Ixioideae are $x = 16$ in *Tritoniopsis*, 13 or 14 in *Romulea*, and 13 in *Geissorhiza* and *Hesperantha*, the two genera possibly the most closely related to *Gladiolus* after *Radinosiphon*.

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# IMPACT OF THE EOCENE ON THE EVOLUTION OF *PINUS* L.[1]

*Constance I. Millar*[2]


## Abstract

*Pinus* evolved in middle latitudes of the Northern Hemisphere in the middle Mesozoic. By the late Cretaceous pines had spread east and west throughout Laurasia, attaining high diversity in eastern Asia, the eastern United States, and western Europe, but having little representation at high northern latitudes. Changing climates in the early Tertiary established warm and humid tropical/subtropical conditions in a broad zone to 70°N throughout middle latitudes. Pines and their relatives disappeared from many middle-latitude areas during this time and were replaced by diverse angiosperm taxa of the boreotropical flora, which were adapted to the equable, tropical climate. The effect of this climate change and spread of boreotropical flora was to displace pines from their former habitats. A hypothesis is defended that pines shifted, during the three warm periods of the Eocene, into three major refugial areas in the Northern Hemisphere: high latitudes, low latitudes, and upland regions of middle latitudes, especially in western North America. Some of these refugial areas (e.g., Mexico/Central America) underwent active volcanism and mountain-building in the Eocene and became secondary centers of pine diversity. Many phylogenetic patterns within *Pinus* can be traced to this fragmentation, isolation, and evolution in Eocene refugia. Subsections *Oocarpae* and *Sabinianae* appear to have originated from refugia in Mexico and Central America. Older subsections such as *Sylvestres*, *Ponderosae*, *Contortae*, and *Strobi* were distributed over several *refugia*; subsections *Leiophyllae*, *Australes*, and *Cembroides* evolved in southern refugia in North America; and *Canarienses* evolved in southern refugia along the Tethys seaway in Eurasia. Following the cooling and drying of the climate at the end of the Eocene, many angiosperm taxa of the boreotropical flora became extinct and pines recolonized middle latitudes, a zone they have occupied to the present. Migration out of refugia provided additional opportunities for hybridization and introgression, as formerly isolated lineages expanded and met.


The past two decades have seen an explosion of information on the paleohistory of the Earth. Evidence on plate tectonics has clarified the position of continents in different ages, continental geomorphology, and the dynamics of inland seaways and changing coastlines. Physical and biological evidence has been used to infer paleoclimates with finer resolution in time and space. New fossil discoveries have added to the record of past vegetation, and new diagnostics for identifying taxa have led to systematic revisions of many fossil floras. The widespread use of radioisotope dating has added precision to determining the ages of fossil floras.

This information, together with phylogenetic analyses of extant taxa, has contributed new insights and a revised understanding of evolution for many plant groups. In pines (family Pinaceae, genus *Pinus* L.), major syntheses have focused on two time periods in the history of the genus. Studies on the Mesozoic history of the pine family, and especially *Pinus*, have significantly changed our understanding of the origin of the genus (Miller, 1976, 1977, 1982, 1988; Robison, 1977; Blackwell, 1984; Stockey & Ueda, 1986; Stockey & Nishida, 1986). Similarly, studies on the Quaternary history of pines have led to new interpretations about the impact of recent paleohistoric events on the genetic structure and evolutionary relationships of extant species (Critchfield, 1984, 1985).

The broad-scale events that influenced the evolution of the genus between its origins in Mesozoic (Table 1) and its present diversity remain obscure. How did important secondary centers of pine diversity in Mexico, western North America, and eastern Asia originate? How do these areas relate to the primary centers of origin for the genus? What events triggered the diversifications of taxa within the genus, and how have historical events influenced current and fossil distribution? Although there have been important contributions to understanding regional biogeography and evolution of pines in the Tertiary (Eguiluz Piedra, 1985, 1988; Axelrod, 1986; Lauria, 1991), the impact of Pa-

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TABLE 1. Approximate ages and durations of geological eras from the Mesozoic to present.

| Era | Period | Epoch | Duration (millions of years) | Millions of years ago |
|---|---|---|---|---|
| Cenozoic | Quaternary | Holocene | Approximately the last 10,000 years | |
| | | Pleistocene | 2.4 | 2.5 |
| | Tertiary | | | |
| | Neogene | Pliocene | 4.5 | 7 |
| | | Miocene | 19 | 26 |
| | Paleogene | Oligocene | 12 | 34[1] |
| | | Eocene | 16 | 54 |
| | | Paleocene | 11 | 65 |
| Mesozoic | Cretaceous | | 71 | 136 |
| | Jurassic | | 54 | 190 |
| | Triassic | | 35 | 225 |

[1] The Oligocene–Eocene boundary is accepted to be 34 Ma, coinciding with the terminal Eocene event. Authors publishing before the middle 1970s and some current ones accept the boundary as 38 Ma.

leogene (Paleocene through Oligocene) events, especially the Eocene, on the evolution of the genus as a whole has not been analyzed. In this paper, I attempt to synthesize recent information on plate tectonics, climate, fossils, and biogeography of pines and other dominant plant groups as they affected pine evolution. From this synthesis, I argue that the Eocene was one of the most important phases in pine evolution.

## SYSTEMATICS AND CURRENT BIOGEOGRAPHY OF *PINUS*

The genus *Pinus* is one of the most widely distributed genera of trees in the Northern Hemisphere. Pines occur predominantly at middle latitudes (30°–55°N), but important centers of pine species also exist at high (> 55°N) and low latitudes (< 30°N) (Figs. 1, 2; Critchfield & Little, 1966). Pines are abundantly represented in North America, Central America, Europe, and Asia, with some taxa extending into northern Africa. Within their range, pines occur in diverse habitats, extend from sea level to 3,700 m, and dominate natural vegetation in many regions. They are absent from hot, wet, tropical environments, where they are poor competitors with other taxa (Mirov, 1967; Bond, 1989). At tropical latitudes, pines occur only in uplands or semi-arid regions.

*Pinus* contains more species than any other genus of conifers, although *Podocarpus* may rival it. Pines have been recognized since Classical times, and more than 40 classification systems have been proposed (Critchfield & Little, 1966; Mirov, 1967; Little & Critchfield, 1969; Price, 1989; Millar & Kinloch, 1991). The most widely accepted is the system of Little & Critchfield (1969), which built upon and modified the classification of Shaw (1914, 1924). Little & Critchfield (1969) divided *Pinus* into 3 subgenera, 5 sections, 15 subsections, and 94 species (Fig. 3). They updated the classification by incorporating new types of information based on genetic data, especially from contemporary studies on hybridization and biochemical variation. Thus, their classification implicitly suggests phylogenetic relationships and common origins of species and groups of species. Since the time of Little and Critchfield's classification, several new species have been described, especially from species-rich and as yet still incompletely known regions such as Mexico. In this paper, I accept Little and Critchfield's authority for species, and cite authors of taxonomic names only for those taxa outside of their system. I also accept most aspects of their

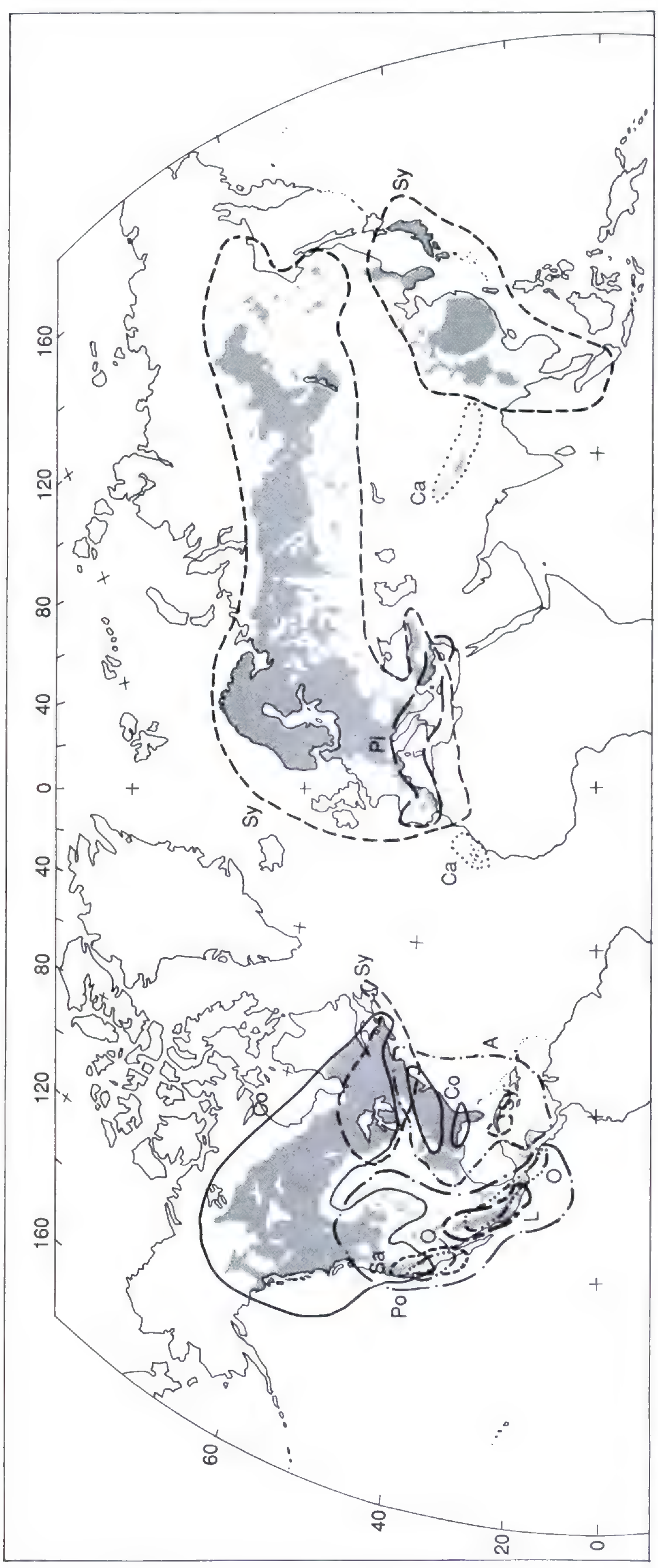



FIGURE 1. Distribution of *Pinus* subgenus *Pinus*, showing general locations of subsections within the subgenus. A = *Australes*, Ca = *Canarienses*, Co = *Contortae*, L = *Leiophyllae*, O = *Oocarpae*, Pi = *Pinеae*, Po = *Ponderosae*, Sa = *Sabinianae*, Sy = *Sylvestres*.

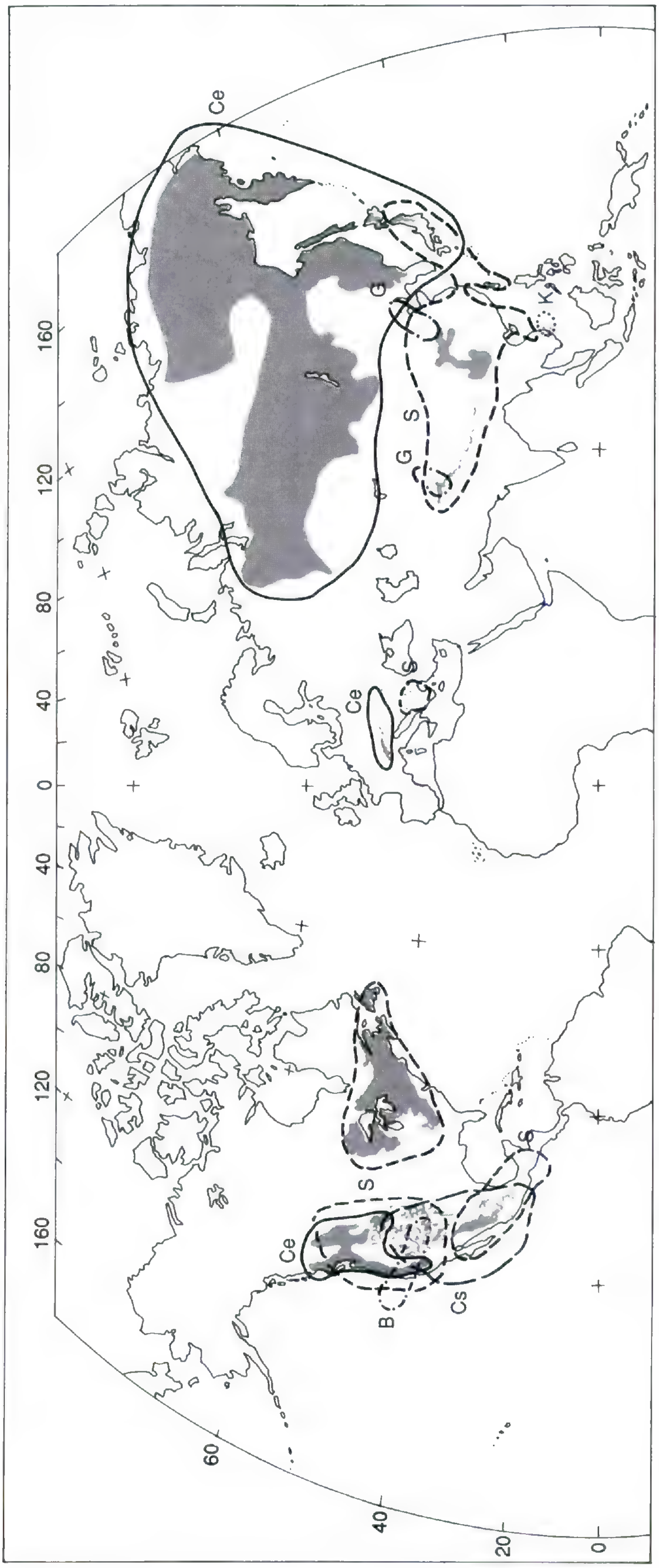



FIGURE 2. Distribution of *Pinus* subgenus *Strobus* and subgenus *Ducampopinus*, showing general locations of subsections within the subgenus. B = *Balfourianae*, Ce = *Cembrae*, Cs = *Cembroides*, G = *Gerardianae*, S = *Strobi*, K = *Krempfiani* (Ducampopinus).

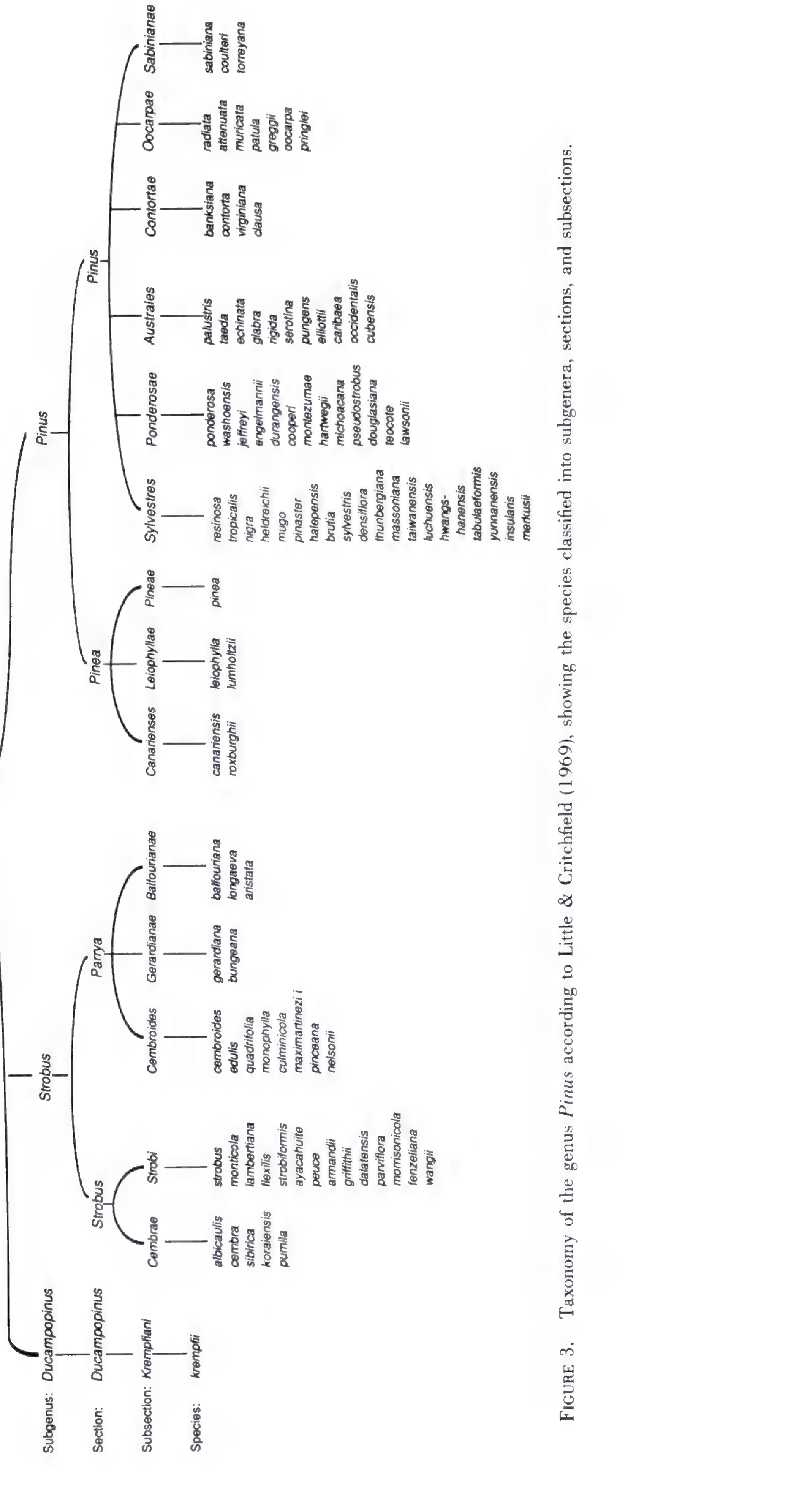



FIGURE 3. Taxonomy of the genus *Pinus* according to Little & Critchfield (1969), showing the species classified into subgenera, sections, and subsections.

classification as the best presently available hypothesis of phylogenetic relationships among the groups of extant taxa.

## Mesozoic Biogeography

### ORIGIN OF PINES

The prevailing hypothesis until the mid-1970s on the origin of the genus relied on the contemporary interpretation of Mesozoic fossil flora and the prevailing theories of the origin of cool temperate vegetation (Chaney, 1940; Mirov, 1967; Mirov & Hasbrouck, 1976). Fossil pines had been described from Triassic, Jurassic, and abundant Cretaceous locales, with pines especially abundant and diverse at high northern paleolatitudes. Mirov's widely cited interpretation dated the genus to the late Paleozoic or earliest Mesozoic, with its origin centered in a far-northern circumpolar continent known as Beringia. According to Mirov, the subsequent evolution of pines unfolded in a steady and progressive migration southward during the Mesozoic and Tertiary, culminating in a final southward thrust toward the equator during the Pleistocene.

This interpretation was cast into doubt by systematic revisions of Mesozoic coniferous fossils. Alvin, Creber, Miller, Stockey, and others compared internal anatomy of fossil and extant pinaceous cones and found four diagnostic traits that characterize *Pinus* (summarized in Miller, 1976). When previously described fossils were reanalyzed, many that were originally ascribed to *Pinus* were reclassified in the extinct pinaceous genera *Pityostrobus* and *Pseudoaraucaria*. This applied to all the known pinaceous remains from the Triassic and Jurassic, and many from the Cretaceous. In particular, all of the high-latitude macrofossils, primarily in the collections of Heer, 1868–1883, originally treated as *Pinus* were reclassified, in some cases, even as angiosperms.

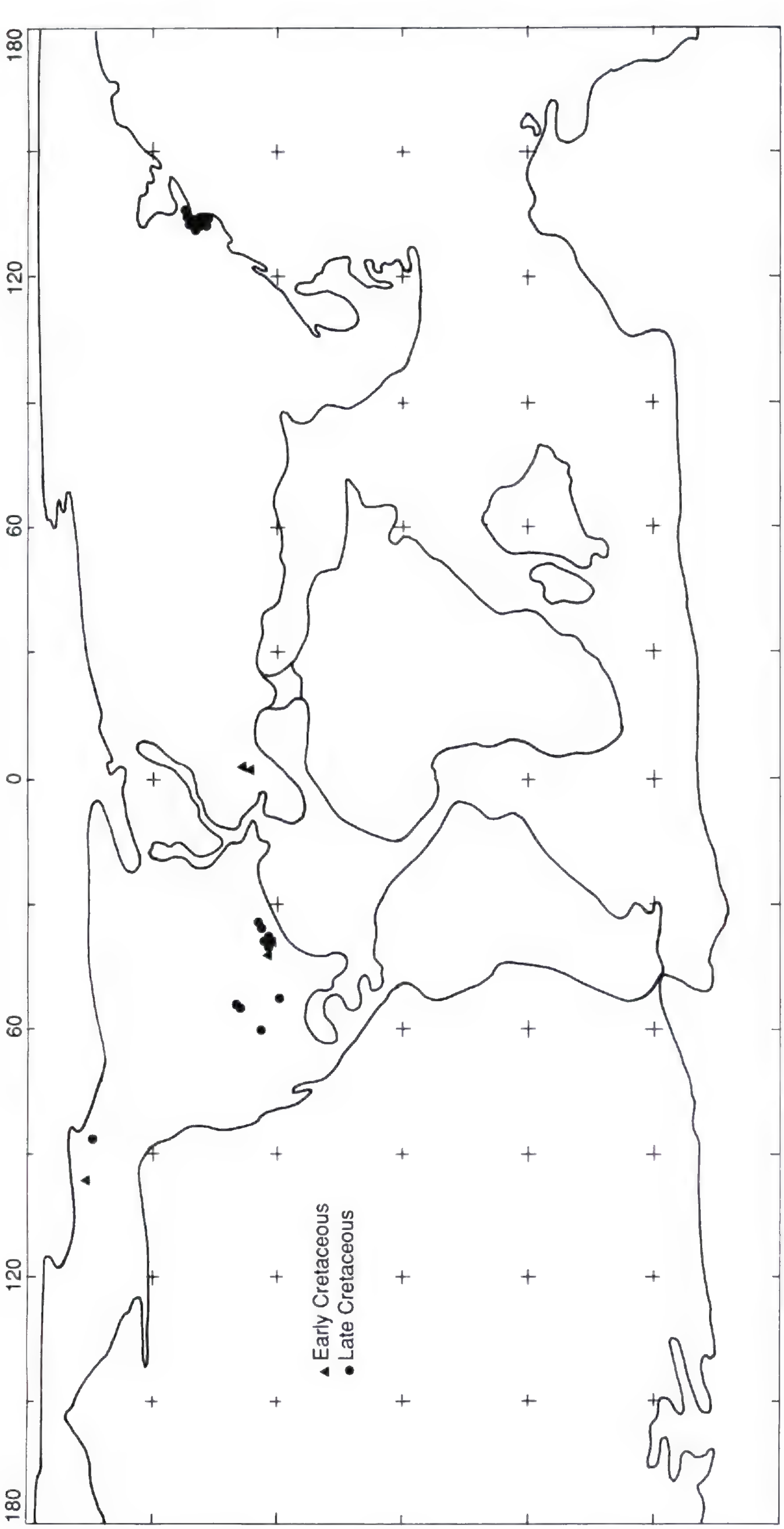
The revisions, combined with new fossil discoveries in the last two decades, result in a Cretaceous fossil record of about 25 species of pines from eight Northern Hemisphere regions (Table 2; Fig. 4). About half are known from petrified cones whose internal anatomy has been confirmed as *Pinus*. Others are needle, wood, or pollen fossils, generally accepted to be *Pinus*. Of special note is the distribution of these fossil pines. Although a geographic bias may be expected due to proximity of fossil locations to active paleobotanists, fossil pines occur at middle and a few high latitudes, widely spread east and west, with apparent centers in the northeastern United States, Japan, and western Europe. The earliest known pine, *P. belgica*, from the early Cretaceous (about 130 Ma) was found in Belgium. Pollen of an early Cretaceous pine was also found in amber deposits from Alaska (Langenheim et al., 1960). All other pine fossils are known from middle to late Cretaceous deposits.

The taxonomic diversity of fossil pines in the Cretaceous record is broad; two major subgenera and five subsections are represented. The origin of the genus is thought to be early-middle Mesozoic, although probably not the Paleozoic as suggested by Mirov (Miller, 1976; Eguiluz Piedra, 1985; Axelrod, 1986; Millar & Kinloch, 1991). A major change from Mirov's thinking concerns the location of the center of origin of the genus and the paths of subsequent radiation. At the beginning of the Mesozoic, there was one land mass, Pangaea (Smith et al., 1981). By the early Jurassic, a northern supercontinent, Laurasia, separated and began to drift from a southern continent, Gondwanaland. Although there may have been more land above sea in northern latitudes than at present (Wolfe, 1985) little evidence exists for a circumpolar continent, Beringia, that would have supported the origin of pines (Hickey et al., 1983; Eguiluz Piedra, 1985; Wolfe, 1985).

Most importantly, no fossil evidence exists for a high-latitude Mesozoic center of origin for pines. Mesozoic pine fossils occur between 31°N and 50°N latitude, with only two records from higher latitudes (Table 2). Similarly, fossils of six species of *Pseudoaraucaria* and over 20 species of *Pityostrobus*, genera considered most closely related to *Pinus* and most likely to have been the ancestral gene pool to *Pinus*, also occurred exclusively at middle latitudes, concentrated in eastern North America and western Europe (Miller, 1976, 1988). Hence, a circumpolar origin for *Pinus* is unsupported, and pine origins in middle latitudes are more likely. The regions of the northeastern United States and western Europe, which would have been contiguous in the early and middle Mesozoic (Smith et al., 1981), are the current candidates for the center of origin of the genus (Miller, 1976; Eguiluz Piedra, 1985; Axelrod, 1986; Millar & Kinloch, 1991). Alternatively, the diversity of Cretaceous pines and *Pityostrobus* in Japan suggests that pines might have evolved in eastern Asia.

### DISTRIBUTION OF PINES AND CLIMATE OF THE LATE CRETACEOUS

To understand the impact of the early Tertiary on pines, it is important to stress the Late Cretaceous distribution of pines and the prevailing cli-




Base map © Cambridge University

FIGURE 4. Distribution of pine fossils from Cretaceous deposits, mapped by estimated paleocoordinates on map of the late Cretaceous world. Base map Press 1981, taken from Smith, Hurley & Briden, *Phanerozoic paleocontinental world maps*.

TABLE 2. Distribution and affinities of fossil pines from Cretaceous deposits listed in approximate order of age (old to young). Paleocoordinates from Smith et al. (1981).

| Identification | Affinity | Location | Latitude/longitude | | Age (Ma) | Reference |
|---|---|---|---|---|---|---|
| | | | Current | Paleo | | |
| *P. belgica* | *Sylvestres* | Belgium, Wealden | 50°N 4°E | 39°N 5°E | 130 | Alvin (1960) |
| *Pinus* pollen | genus | Alaska, Kuk River | 70°N 160°W | 80°N 100°W | Early | Langenheim et al. (1960) |
| *Pinus* pollen | genus | Maryland | 39°N 79°W | 32°N 41°W | Late Early | Brenner (1963) |
| *Pinus* pollen | genus | Delaware | 39°N 75°W | 31°N 39°W | Late Early | Groot et al. (1961) |
| *P. wohlgemuthi* | subg. *Pinus* | France | 48°N 4°E | 35°N 18°E | Late Early | Alvin (1960) |
| *P. ponderosoides* | *Ponderosae-Australes* | Mississippi, Prentiss Co. | 34°N 88°W | 31°N 52°W | Early Late | Blackwell (1984) |
| *Pinus* pollen | *Sylvestres* | Minnesota | 44°N 95°W | 40°N 55°W | Early Late | Pierce (1957) |
| *P. clementsii* | *Sylvestres* | Minnesota | 44°N 95°W | 40°N 55°W | Late | Chaney (1954) |
| *Pinus* sp. | *Sylvestres* | Delaware | 39°N 75°W | 32°N 40°W | Late | Penny (1947) |
| *P. triphylla* | *Sylvestres/Leiophyllae* | Massachusetts | 41°N 71°W | 33°N 35°W | Late | Robison (1977) |
| | | New York, Staten Island | 41°N 74°W | 34°N 37°W | Late | Hollick & Jeffrey (1909) |
| | | Japan, Hokkaido | 42°N 142°E | 48°N 135°E | Late | Stockey & Nishida (1986) |
| *P. tetraphylla* | *Sylvestres* | Japan, Hokkaido | 42°N 142°E | 48°N 135°E | Late | Stockey & Nishida (1986) |
| *P. bifoliata* | *Sylvestres* | Japan, Hokkaido | 43°N 142°E | 49°N 135°E | Late | Stockey & Nishida (1986) |
| *P. pseudotetraphylla* | *Sylvestres* | Japan, Hokkaido | 43°N 142°E | 49°N 135°E | Late | Stockey & Nishida (1986) |
| *P. flabellifolia* | *Canarienses* | Japan, Hokkaido | 43°N 142°E | 49°N 135°E | Late | Ogura (1932), Stockey & Nishida (1986) |
| *P. quenstedti* | *Ponderosae* | Kansas | 38°N 99°W | 34°N 61°W | Late | Lesquereux (1883) |
| *P. quinquefolia* | *Ponderosae* | Massachusetts | 41°N 71°W | 33°N 35°W | Late | Penny (1947), Robison (1977) |
| | | New York, Staten Island | 41°N 74°W | 34°N 37°W | Late | Hollick & Jeffrey (1909) |
| | | Japan, Hokkaido | 42°N 142°E | 48°N 135°E | Late | Stockey & Nishida (1986) |
| *P. pachydermata* | subg. *Pinus* | Japan, Hokkaido | 42°N 142°E | 48°N 135°E | Late | Ueda & Nishida (1982) |
| *P. pseudostrobifolia* | *Ponderosae* | Japan, Hokkaido | 43°N 142°E | 49°N 135°E | Late | Ogura (1932), Stockey & Nishida (1986) |
| *P. pseudoflabellifolia* | subg. *Pinus* | Japan, Hokkaido | 44°N 142°E | 50°N 136°E | Late | Ueda & Nishida (1982) |
| *P. harborensis* | *Ponderosae* | Japan, Hokkaido | 44°N 142°E | 50°N 136°E | Late | Stockey & Nishida (1986) |
| *P. hokkaidoensis* | *Ponderosae/Leiophyllae* | Japan, Hokkaido | 44°N 142°E | 50°N 136°E | Late | Stockey & Ueda (1986) |
| *P. cliffwoodensis* | *Australes/Ponderosae* | New Jersey, Magothy | 40°N 74°W | 32°N 38°W | Late | Miller & Malinky (1986) |

TABLE 2. Continued.

| Identification | Affinity | Location | Latitude/longitude | | Age (Ma) | Reference |
|---|---|---|---|---|---|---|
| | | | Current | Paleo | | |
| *Pinus* sp. | subg. *Strobus* | New York, Staten Island | 41°N 74°W | 34°N 37°W | Late | Jeffrey (1908) |
| *P. magothensis* | *Strobi* | Delaware | 39°N 75°W | 31°N 38°W | Late | Penny (1947) |
| *P. yezoensis* | subg. *Strobus* | Japan, Hokkaido | 43°N 142°E | 49°N 135°E | Late | Stopes & Kershaw (1910) |
| *Pinus* pollen | genus | Alaska, Colville River | 70°N 151°W | 75°N 88°W | Late | Frederiksen et al. (1988) |

mate at the end of the Mesozoic. By the Late Cretaceous, pines had reached eastern and western edges of Laurasia and occurred at middle latitudes in many locations between these extremes (Table 2; Fig. 4). The widespread distribution of pines in Laurasia by this time indicates that wherever within middle latitudes they originated, their main route of migration was east and west, and not predominately southward, as Mirov suggested. Migration from eastern North America to western Europe was not impeded until late in the Mesozic, by which time Laurasia had begun to split into North America and Europe. Laurasia severed first in the south and last in the north. High-latitude connections in the North Atlantic became increasingly reduced toward the end of the Mesozoic, and low seas may have covered the land (Ziegler et al., 1983; Tiffney, 1985a; Parrish, 1987). This region would have provided only minor corridors for pine migration. Evidence also exists for land connections at high latitudes in the Bering Sea region between Siberia and Alaska being used as corridors for temperate-adapted flora.

Within the new continents, continuing east–west migration in the late Cretaceous must have been hindered by seaways that extended the full north–south length of the continents (Kurten, 1966; Tiffney, 1985a). These seaways divided the continents into separate phytogeographic provinces, creating greater floristic affinities between eastern North America and western Europe, and western North America and eastern Asia, than between the east-west parts of each continent (Wolfe, 1975; Tiffney, 1985a).

The Late Cretaceous was a time of climatic quiescence and equability (Parrish, 1987; Upchurch & Wolfe, 1987; McGowran, 1990). Sea levels were high, and tectonic activity low, creating stable global climates. Although the breakup of Pangaea had commenced, paleocontinents were still relatively undispersed, resulting in average temperatures in the middle and high latitudes about 10°-20°C warmer than the present (Savin, 1977; Shackleton & Boersma, 1981; Parrish, 1987; Upchurch & Wolfe, 1987). Evidence on rainfall in the Cretaceous inferred from foliar physiognomy of angiosperms indicates that rainfall patterns were zonal. The Northern Hemisphere had a humid region around the paleoequator, a dry zone at low-middle latitudes, and a zone of higher rainfall above 45°N (Parrish, 1987). In general, however, latitudinal gradients were shallower, and changes in temperature with latitude were about ½–⅓ of present gradients (Parrish, 1987; Upchurch & Wolfe, 1987). Temperature and rainfall appear to have

been stable annually, with little seasonality at latitudes below 45°N (Upchurch & Wolfe, 1987). At higher latitudes, day lengths and precipitation apparently varied seasonally. The major cordillera of the Northern Hemisphere were not developed, or existed only at low elevations. Volcanic activity was minor, so there were few orographic effects on climate and little regional diversity in climate.

## Early Tertiary Biogeography

### CHANGING CLIMATES

Major changes in climate and vegetation characterized the early Tertiary (Wolfe, 1990). Although these events have long been discussed by paleobotanists interested in angiosperm evolution (Wolfe, 1975; Tiffney, 1985a, b; Friis et al., 1987), their impact on conifer evolution has not been analyzed. In general, average temperatures rose and rainfall increased in the early Tertiary. The trends toward increasing temperature and humidity started in the early Paleocene and continued into the Eocene, reaching maxima in the early Eocene, about 52 Ma. By this time, average temperatures had increased 5°–7°C above the Late Cretaceous (Savin, 1977), and tropical/subtropical conditions apparently extended at many middle and high latitudes to 70°–80°N (Wolfe, 1985; McGowran, 1990). High temperatures and humidity, however, did not persist stably throughout the Eocene. Although the late Paleocene/early Eocene (54–52 Ma) was the warmest and wettest period, there were at least two other warm periods, from about 46 to 42 Ma, and about 36 to 34 Ma, separated by cooler intervals that were approximately equal in duration to the warm periods (Fig. 6; Wolfe, 1978, 1985; McGowran, 1990). Average annual temperatures may have fluctuated as much as 7°–10°C between warm and cool periods of the Eocene (Wolfe, 1978). Several causes for these climatic developments have been suggested, including major tectonic events, changes in sea level, and submarine volcanism resulting in accumulation of atmospheric carbon dioxide and greenhouse heating (Wolfe, 1978; Parrish, 1987; McGowran, 1990; Kerr, 1991). Alternatively, large amounts of carbon dioxide may have been produced as a result of ocean-atmosphere interactions following a major extraterrestrial impact at the Cretaceous/Tertiary boundary (O'Keefe & Ahrens, 1989), which led to greenhouse warming (Wolfe, 1990).

Although latitudinal gradation was not great, the pattern in the Eocene differed from both the Cretaceous and the later Tertiary and Quaternary: in general, many low-latitude locations were relatively warm and seasonally dry, middle latitudes were warm and wet, and high latitudes were cool and dry (Parrish, 1987; Wolfe, 1978). Truly arid zones apparently did not exist; there is no evidence for Paleogene arid deserts or tundra (Axelrod, 1979).

Although these general trends in temperature and humidity existed throughout a broad latitudinal zone worldwide, there was geographic heterogeneity in the intensity of conditions. The warm humid zone was widest in North America and western Europe, and narrower in central and eastern Asia (Chaney, 1940; Parrish, 1987; Hsu, 1983). In general, continental elevations were low throughout the Paleogene, and upland areas apparently existed primarily in one middle-latitude region of western North America and in Antarctica (Axelrod, 1966; Wolfe, 1985, 1987; Wolfe & Wehr, 1987; Wing, 1987). In the upland area of western North America, the climate was anomalously temperate compared to other middle-latitude areas. Volcanism and mountain-building in this area during the Eocene also created heterogeneity in local climates and habitats.

### THE ANGIOSPERM BOREOTROPICAL FLORA

The changes in climate during the early Tertiary drastically affected global floristics (Friis et al., 1987; Wolfe, 1975, 1978, 1985). Diverse tropical and subtropical angiosperm floras appeared with increasing geographic representation during the Paleocene and the warm intervals of the Eocene throughout broad zones at middle latitudes in both Northern and Southern Hemispheres. Originally identified from the London Clay formations of England (Reid & Chandler, 1933), similar angiosperm floras have been described from many deposits elsewhere, including western and eastern North America (from the Pacific Coast to Nebraska and Texas; Vermont, Alabama), western and eastern Europe (including England, France, Belgium, Germany, Bulgaria, Ukraine, and Russia), northern Egypt, China, and Japan (Mai, 1970; Graham, 1972; Wolfe, 1975, 1985; Tiffney, 1985a, b). Subtropical assemblages occurred north as far as 70° in Alaska, and at other high-latitude locations in Canada, Greenland, and Siberia (Wolfe, 1977, 1985). In North America, the average zone extended from 30°N to 50°N (Wolfe, 1985). The origin and major radiation of many angiosperm taxa is documented in these diverse floras.

Plant communities in these Paleogene floras were adapted to warm, humid, and equable conditions. These taxa were similar to those found in modern rainforest vegetation of Malaysia and other extant tropical rainforest regions and show comparable adaptations. Common genera include *Engelhard-*

*tia*, *Ficus*, *Pterocarya*, *Nypa*, *Platycarya*, *Wetherellia*, *Alangium*, and *Nyssa*. A few gymnosperms such as *Glyptostrobus*, *Taxodium*, and occasionally *Sequoia* occurred in these floras, but they, too, were apparently adapted to warm, humid conditions.

Recognizing their northern locations and their adaptations to warm, humid conditions, Wolfe (1975, 1977) referred to these widespread angiosperm assemblages as the "boreotropical flora." While this assemblage in no way suggests an organic, indivisible unit, it does imply that similarly adapted individual taxa migrated east and west rapidly and unimpeded, at middle latitudes throughout North America and Eurasia in the early Tertiary. The boreotropical flora reached its greatest development in the warm periods of the Eocene. During cool intervals, its latitudinal extent shrank.

## EOCENE PINES

The early Tertiary radiation of many angiosperm lineages and the migration of angiosperm boreotropical taxa east and west at middle latitudes has many parallels with the late Mesozoic radiation and migration patterns of pines. Boreotropical floras occur in the same locations worldwide during the early Tertiary as pines did in the late Mesozoic. With very few exceptions, pines are not found in boreotropical fossil floras. This prompts the question, where did the pines go?

The Tertiary record of pines begins in the Eocene; no pines are known from the Paleocene. Pines of the earliest Eocene occur primarily in high (65°–80°N) and low (2°N) latitude deposits in North America and Eurasia (Table 3; Fig. 5). High-latitude locations include central Alaska (Wahrhaftig et al., 1969; Dickinson et al., 1987; Fredericksen et al., 1988), Ellsmere Island, Greenland, Iceland, and Spitsbergen (Manum, 1962; Schweitzer, 1974). Low-latitude pines occurred in Borneo (Muller, 1966) and from one low-middle latitude location of the late early Eocene, near San Diego, California (Axelrod, 1986). Pines in these deposits were associated with other pinaceous conifers and with cool temperate angiosperms such as *Betula*, *Alnus*, and *Ulmus*. Ages of these fossils correspond to the first warm humid period of the Eocene (Fig. 6).

Fossil pines from the middle Eocene continue to be represented at high and low latitudes, but appeared for the first time in the Tertiary in middle-high latitude locations in North America and Eurasia. Most of the known fossils from the cool period of the earlier middle Eocene are in western North America, from British Columbia (Miller, 1973; Stockey, 1983, 1984), Washington (Wolfe & Wehr, 1987), Idaho (Axelrod, 1986), and Colorado (Wodehouse, 1933; MacGinite, 1953) (Table 3; Fig. 5). Western North America in general contains some of the richest plant-bearing deposits from the Eocene in the world, and dozens of fossil floras have been described. Only a few of these contain pines and other temperate taxa, and these are all concentrated in northern Idaho, central Wyoming, north to central Idaho, and British Columbia. This is the region that has been identified as an upland area with average elevations of 1,200–1,500 m (Axelrod, 1965; Axelrod & Raven, 1985; Wolfe, 1987). Pine deposits in some of these areas are associated with active volcanos and high elevations (e.g., Bull Run, Thunder Mountain, Axelrod, 1965, 1986; Creede, 2,500 m, Wolfe & Schorn, 1989).

The warm humid period of the middle Eocene is represented by few pine fossils (Table 3). Pine was present at high latitudes in the Mackenzie Delta of Alaska (80°N, Norris, 1982), at low-middle latitudes in Borneo (2°N, Muller, 1966) and southern Alabama (36°N, Gray, 1960), and also at a few middle latitudes in Nevada (50°N, Axelrod, 1966, 1968), within the upland plateau of western North America.

Pine fossils from the subsequent cool period of the later Eocene occurred at middle latitudes in Washington (Miller, 1974), Nevada (Axelrod, 1966, 1968), Colorado (Leopold & MacGinite, 1972; Axelrod, 1986), New Mexico (Leopold & MacGinite, 1972), and Japan (Huzioka & Takahashi, 1970; Tanai, 1970, interpreted by Wolfe, 1985 to be early-late Eocene), Fushun, China (Hsu, 1983), as well as a continuing presence in Borneo (Muller, 1966) and at high latitudes (Norris, 1982) (Table 3).

The latest Eocene marks the final widespread period of tropical conditions at middle latitudes in the Paleogene (Fig. 6). Pine fossils from the late Eocene occur primarily at high latitudes in western Siberia (Dorofeev, 1963), Alaska (Norris, 1982), British Columbia (Hopkins et al., 1972), at low latitudes in Borneo (Muller, 1966), and along the Tethys seaway in southeastern Europe (Chiguriaeva, 1952). Pines from the southeast coast of China, in the provinces of Jiang-su, Zhejian, and Fujian (Hsu, 1983), may also be from this period (Table 3).

## THE TERMINAL EOCENE EVENT AND PINE EXPANSIONS

The end of the Eocene was marked by the most profound climatic event of the Tertiary (Burchardt, 1978; Wolfe, 1978; Parrish, 1987; McGowran,

TABLE 3. Distribution and affinities of fossil pines from Eocene deposits listed in approximate order of age (old to young). Paleocoordinates from Smith et al. (1981).

| Identification | Affinity | Location | Latitude/longitude | | Age (Ma) | Reference |
|---|---|---|---|---|---|---|
| | | | Current | Paleo | | |
| *Pinus* pollen | genus | Alaska, Nenana | 64°N 148°W | 77°N 128°W | 54 | Wahrhaftig et al. (1969) |
| *Pinus* pollen | genus | Alaska, Colville | 70°N 151°W | 80°N 127°W | Early | Frederiksen et al. (1988) |
| *Pinus* ? pollen (bisaccate grains) | genus | Alaska, Death Valley | 65°N 162°W | 80°N 143°W | Early | Dickinson et al. (1987) |
| *Pinus* pollen | genus | Canada, Ellsmere Island | 77°N 84°W | 75°N 18°W | Early | Manum (1962) |
| *Pinus* pollen | genus | Greenland | 70°N 52°W | 60°N 8°W | Early | Manum (1962) |
| *Pinus* pollen | genus | Iceland | 65°N 21°W | 50°N 8°E | Early | Manum (1962) |
| *Pinus* pollen | genus | Spitsbergen | 79°N 14°E | 70°N 20°E | Early | Manum (1962), Schweitzer (1974) |
| *Pinus* pollen | genus | North Dakota, Dunn | 47°N 103°W | 56°N 70°W | Early | Leopold & MacGinite (1972) |
| *Pinus* pollen | genus | Northwestern Borneo | 2°N 110°E | 2°N 110°E | Late Early | Muller (1966) |
| *P. delmarensis* | subg. *Strobus* | Southern California | 33°N 117°W | 42°N 92°W | 47–48 | Axelrod (1986) |
| *Pinus* pollen | *Cembroides* | Southern California | 33°N 117°W | 41°N 92°W | 47–48 | Axelrod & Raven (1985) |
| *Pinus* pollen | *Ponderosae* | Southern California | 33°N 117°W | 41°N 92°W | 47–48 | Axelrod & Raven (1985) |
| *Pinus* pollen | genus | Northeastern China, Fushun | 42°N 124°E | 45°N 118°E | Mid and Late | Sung & Liu (1976), Hsu (1983) |
| *P. ballii* | *Cembroides* | Colorado, Green River | 41°N 109°W | 50°N 80°W | 47 | Wodehouse (1933), Brown (1934) |
| *P. driftwoodensis* | *Sylvestres Ponderosae Australes* | British Columbia, Smithers | 55°N 127°W | 66°N 97°W | 46–47 | Stockey (1983) |
| *P. arnoldii* | *Sylvestres* | British Columbia, Princeton | 50°N 120°W | 61°N 90°W | 46–47 | Miller (1973), Stockey (1984) |
| *P. similkameensis* | subg. *Strobus* | British Columbia, Princeton | 50°N 120°W | 61°N 90°W | 46–47 | Miller (1973) |
| *P. princetonensis* | *Sylvestres* | British Columbia, Princeton | 50°N 120°W | 61°N 90°W | 46–47 | Stockey (1984) |
| *P. andersonii* | *Ponderosae* | British Columbia, Princeton | 50°N 120°W | 61°N 90°W | 46–47 | Stockey (1984) |
| *Pinus* pollen | genus | Washington, Republic | 49°N 118°W | 60°N 87°W | 46–47 | Wolfe & Wehr (1987) |
| *P. balfouroides* | *Balfourianae* | Idaho, Thunder Mountain | 45°N 114°W | 55°N 84°W | 46–47 | Brown (1937), Axelrod (1986) |

TABLE 3. Continued.

| Identification | Affinity | Location | Latitude/longitude | | Age (Ma) | Reference |
|---|---|---|---|---|---|---|
| | | | Current | Paleo | | |
| *Pinus* pollen | genus | Canada, MacKenzie Delta | 69°N 134°W | 80°N 80°W | Mid-Late | Norris (1982) |
| *Pinus* pollen | genus | Alabama, Claiborne Bluffs | 31°N 88°W | 36°N 62°W | Middle | Gray (1960) |
| *P. wheeleri* | *Strobi* | Nevada, Elko | 41°N 116°W | 50°N 90°W | 42 | Axelrod (1968) |
| *P. crossii* | *Balfourianae* | Nevada, Copper Basin | 42°N 115°W | 51°N 89°W | 40–44 | Axelrod (1966) |
| *P. wolfei* | *Sylvestres/ Contortae* | Washington, Little Falls | 47°N 123°W | 60°N 93°W | Early Late | Miller (1974) |
| *P. alvordensis* | *Contortae* | Nevada, Bull Run | 41°N 117°W | 50°N 91°W | 38 | Axelrod (1968) |
| *Pinus* pollen | genus | New Mexico, Bernalillo | 35°N 107°W | 44°N 80°W | 38 | Leopold & MacGinite (1972) |
| *Pinus* sp. | genus | Southwestern Japan, Ube | 34°N 130°E | 40°N 130°E | Early Late | Huzioka & Takahashi (1970) |
| *Pinus* sp. | genus | Japan, Kushiro | 43°N 144°W | 50°N 135°E | Early Late | Tanai (1972) |
| *Pinus* pollen | genus | Colorado, Chaffee | 39°N 105°W | 49°N 76°W | 36–37 | Leopold & MacGinite (1972) |
| *Pinus* pollen | genus | British Columbia, Parsnip River | 55°N 122°W | 66°N 90°W | 35 | Hopkins et al. (1972) |
| *Pinus* sp. | genus | Siberia, Tavda River | 58°N 65°E | 52°N 58°E | Late | Dorofeev (1963) |
| *Pinus* sp. | genus | Siberia, Ob River | 57°N 85°E | 54°N 75°E | Late | Dorofeev (1963) |
| *Pinus* sp. | genus | Siberia, Tym River | 60°N 82°E | 55°N 73°E | Late | Dorofeev (1963) |
| *P. spinosa* | *Sylvestres/ Ponderosae* | Siberia, Irtysch River | 57°N 75°E | 52°N 67°E | Late | Dorofeev (1963) |
| *Pinus* pollen | genus | Ukraine, River Don | 47°N 40°E | 35°N 38°E | Late | Chiguriaeva (1952) |
| *P. sturgisii* | *Strobi* | Colorado, Florrissant | 39°N 105°W | 48°N 76°W | 34–35 | MacGinite (1953), Axelrod (1986) |
| *P. florrissantii* | *Strobi* | Colorado, Florrissant | 39°N 105°W | 48°N 76°W | 34–35 | MacGinite (1953), Axelrod (1986) |
| *P. wheeleri* | *Strobi* | Colorado, Florrissant | 39°N 105°W | 48°N 76°W | 34–35 | MacGinite (1953), Axelrod (1986) |
| *Pinus* pollen | genus | Southeastern China | 25–35°N 120°E | 28–34°N 118°E | Late | Hsu (1983) |

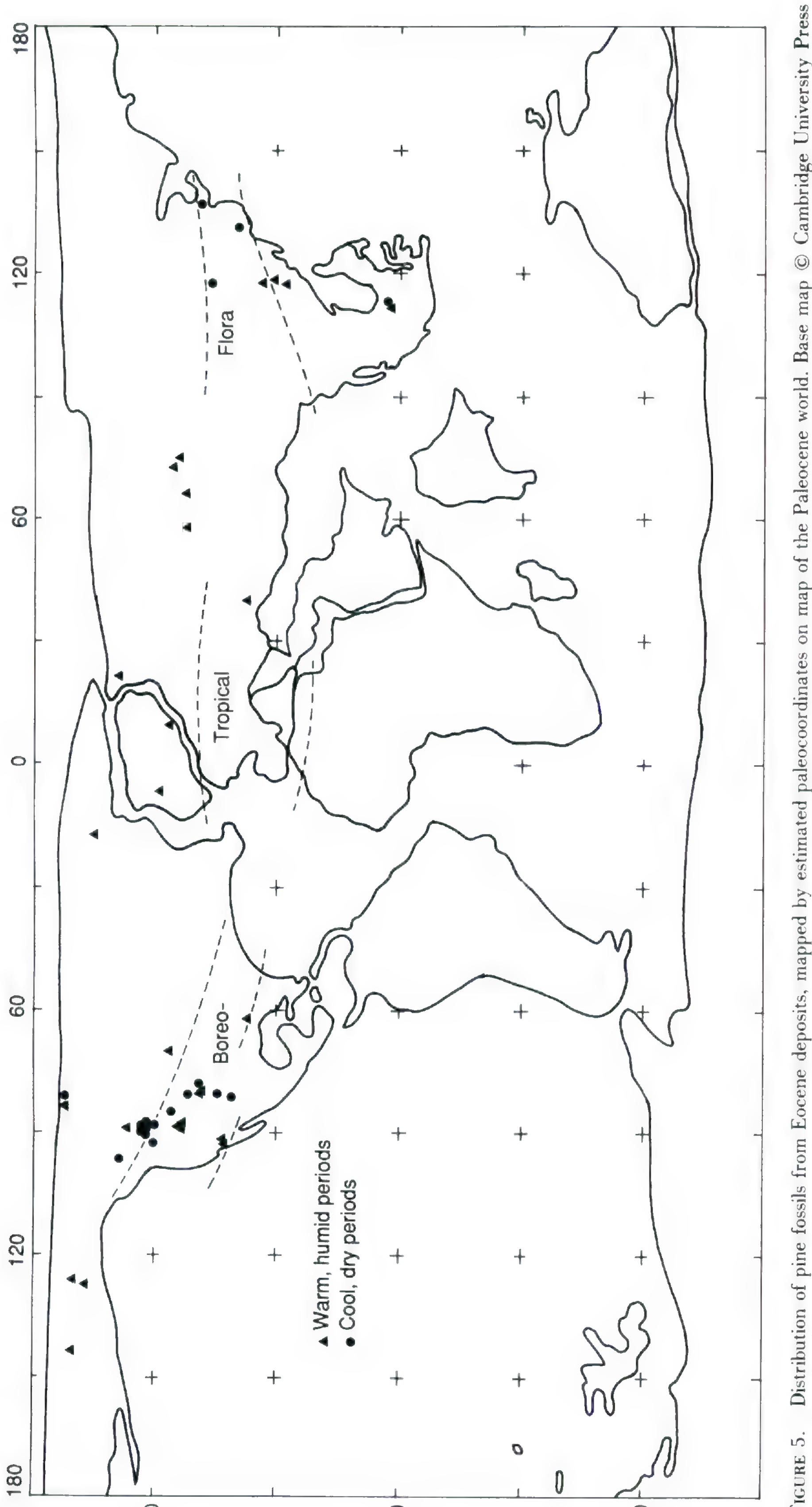



FIGURE 5. Distribution of pine fossils from Eocene deposits, mapped by estimated paleocoordinates on map of the Paleocene world. Base map © Cambridge University Press 1981, taken from Smith, Hurley & Briden, *Phanerozoic paleocontinental world maps*.

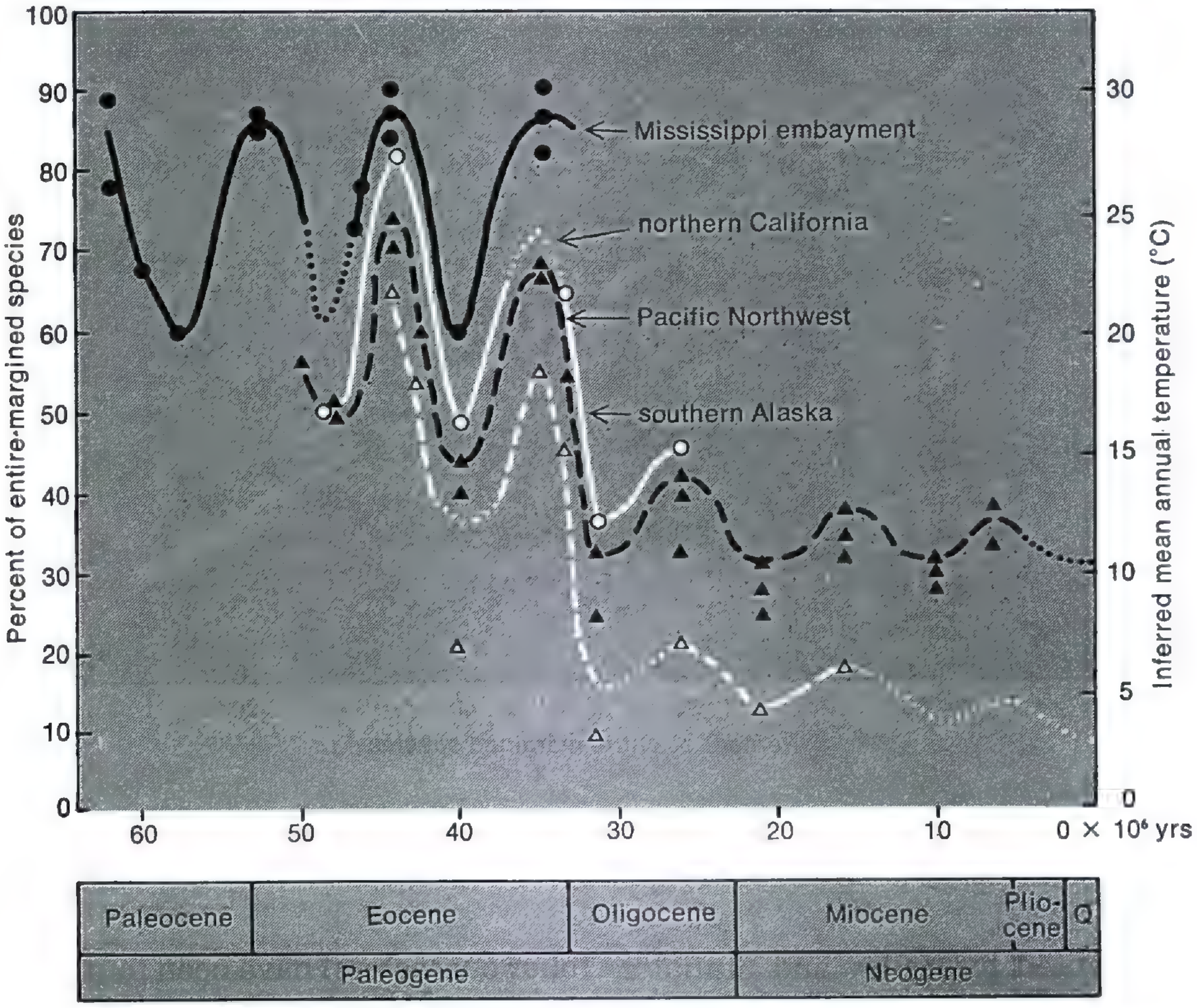



FIGURE 6. Estimated temperatures from four latitudes in North America during the Tertiary (based on percentage of entire leaves), indicating the warm and cool episodes in the Eocene and the drop in temperature at the end of the Eocene (terminal Eocene event). From Wolfe (1978). Reprinted by permission of *American Scientist*, journal of Sigma Xi, The Scientific Research Society.

1990). The fluctuations from warm to cool periods during the Eocene were minor compared to the drop in regional temperatures at the end of the Eocene. Average annual temperatures dropped approximately 10°–13°C, in some areas over only one million years (Fig. 6). The decline in average temperatures was accompanied by a large decrease in rainfall and increase in seasonality. Whereas in the Eocene the mean annual range of temperatures (seasonality) is estimated as only 3°–5°C, in the early Oligocene it is estimated as 25°C—about twice the range of the present (Wolfe, 1971). In many parts of the world, complex continental climate patterns developed, possibly for the first time, and continental ice sheets first occurred in the Oligocene (McGowran, 1990). Extensive volcanism and mountain-building in the Rocky Mountains, Himalayas, and Mexican ranges created local climatic diversity. Major tectonic events have been associated with the climatic cooling at the end of the Eocene with two schools of thought on their effect. One line of evidence suggests that changing positions of the Earth's continents and oceans had direct effects on the Earth's climate, leading to major cooling (Barron, 1985; McGowran, 1990). Another possibility is that the formation of giant uplifted plateaus in southern Asia and the American West led to accelerated chemical weathering, a decline in atmospheric carbon dioxide, and a "greenhouse cooling" effect (Ruddiman & Kutzback, 1989, 1991).

This terminal Eocene event (Wolfe, 1978) was marked by widespread extirpation of boreotropical angiosperm taxa from many middle latitudes worldwide, leaving only remnants in a few areas where the climate presumably remained mild. The extinctions of boreotropical floras were mirrored by great expansion of pines and other cool-adapted taxa into many middle-latitude locations. Many of the same fossil-bearing sites that contained boreotropical taxa in their late Eocene horizons were dominated by cool-temperate conifer taxa in early Oligocene horizons. In some localities, this change occurred in only one million years (Axelrod, 1965).

The existing record suggests that pines made their first Tertiary appearance at many middle-latitude locations during the Oligocene (Table 4; Fig. 7), recolonizing areas where they had occurred

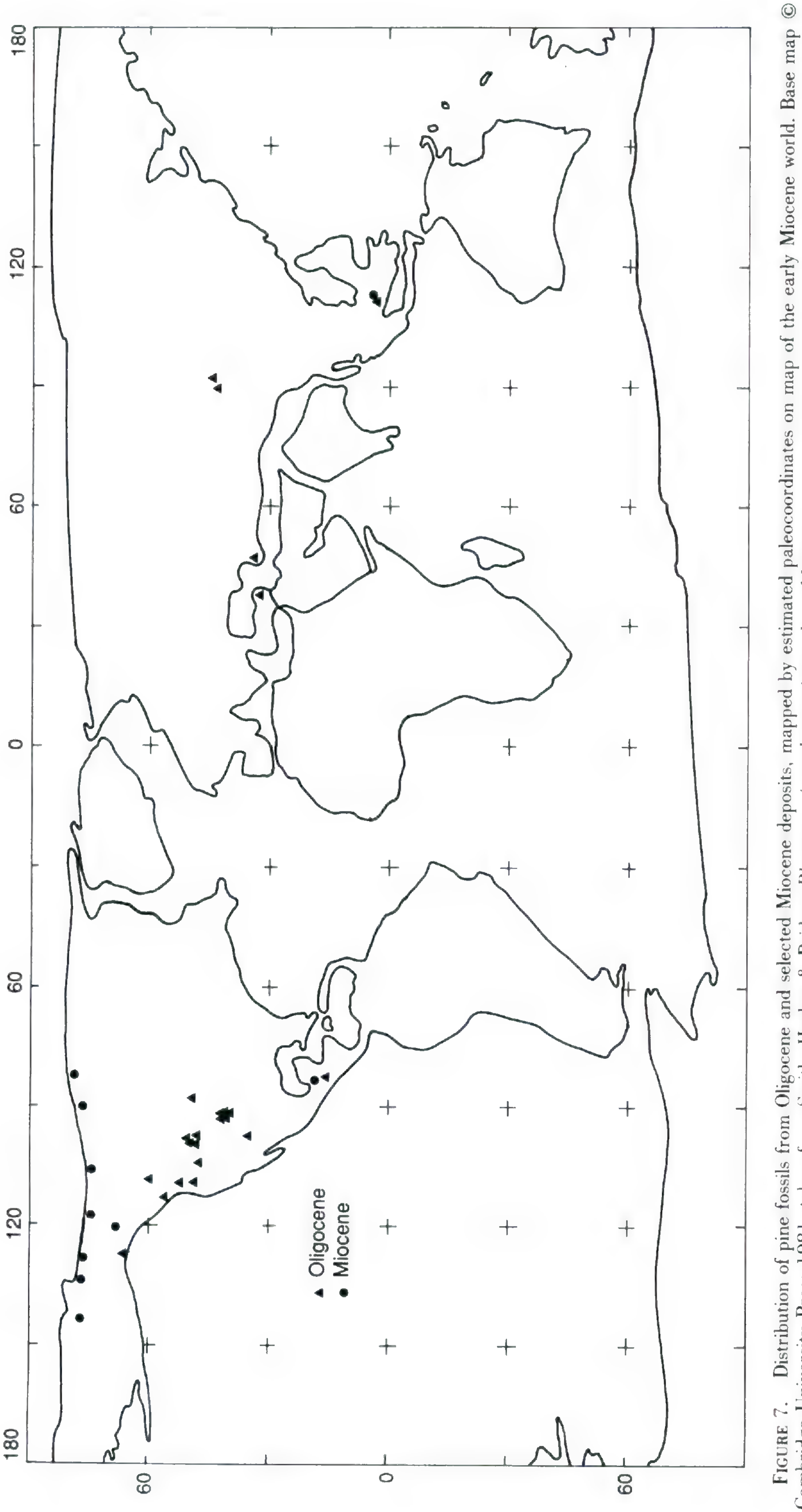



FIGURE 7. Distribution of pine fossils from Oligocene and selected Miocene deposits, mapped by estimated paleocoordinates on map of the early Miocene world. Base map © Cambridge University Press 1981, taken from Smith, Hurley & Briden, *Phanerozoic paleocontinental world maps*.

TABLE 4. Distribution and affinities of fossil pines from Oligocene deposits listed in approximate order of age (old to young). Paleocoordinates from Smith et al. (1981).

| Identification | Affinity | Location | Latitude/longitude | | Age (Ma) | Reference |
|---|---|---|---|---|---|---|
| | | | Current | Paleo | | |
| *Pinus* pollen | genus | Oregon, Bridge Creek | 44°N 118°W | 47°N 105°W | 31 | Wolfe (1981), Mason (1927) |
| *Pinus* pollen | genus | Oregon, Lyons | 45°N 123°W | 49°N 110°W | 31 | Wolfe (1981) |
| *Pinus* pollen | genus | North Dakota, Dunn County | 47°N 103°W | 48°N 88°W | Early | Leopold & MacGinite (1972) |
| *Pinus* pollen | genus | Montana, Ruby Basin | 45°N 112°W | 46°N 100°W | 32–36 | Becker (1961), Wolfe (1977) |
| *P. crossii* | *Balfourianae* | New Mexico, Hillsboro | 33°N 108°W | 34°N 98°W | 32 | Axelrod & Bailey (1976) |
| *Pinus* pollen | genus | British Columbia, Australian Creek | 56°N 126°W | 60°N 110°W | Early | Piel (1971), Rouse & Matthews (1979) |
| *P. escalatensis* | *Contortae* | British Columbia, Escalante Island | 50°N 127°W | 56°N 115°W | Early–Late | Banks et al. (1981) |
| *Pinus* pollen | genus | Northwestern Borneo | 2°N 110°E | 5°N 110°E | Early–Late | Muller (1966) |
| *Pinus* pollen | genus | Gulf of Alaska | 60°N 145°W | 68°N 128°W | Late | Wolfe (1972, 1977) |
| *P. buchananii* | *Ponderosae* | Washington, Olympic | 48°N 123°W | 52°N 110°W | Late | Underwood & Miller (1980) |
| *P. avonensis* | *Ponderosae* | Montana, Avon | 47°N 113°W | 50°N 100°W | Late? | Miller (1969) |
| *P. anthrarivus* | *Strobi* | Idaho, Coal Creek | 45°N 114°W | 47°N 103°W | 29 | Axelrod (1986) |
| *P. balfouroides* | *Balfourianae* | Idaho, Coal Creek | 45°N 114°W | 47°N 103°W | 29 | Axelrod (1986) |
| *Pinus* pollen | genus | Montana, Beaverhead Basin | 45°N 113°W | 47°N 102°W | Late | Becker (1961), Leopold & MacGinite (1972) |
| *Pinus* pollen | genus | Colorado, Chaffee | 39°N 105°W | 40°N 93°W | Late | Leopold & MacGinite (1972) |
| *P. crossii* | *Balfourianae* | Colorado, Creede | 38°N 105°W | 39°N 93°W | 27 | Schorn & Wolfe (1989) |
| *P. riograndе* | *Ponderosae* | Colorado, Creede | 38°N 105°W | 39°N 93°W | 27 | Schorn & Wolfe (1989) |
| *P. sanjuanensis* | *Cembroides* | Colorado, Creede | 38°N 105°W | 39°N 93°W | 27 | Axelrod (1986), Schorn & Wolfe (1989) |
| *Pinus* sp. (cf. *alvordensis*) | *Contortae* | Colorado, Creede | 38°N 105°W | 39°N 93°W | 27 | Axelrod (1986), Schorn & Wolfe (1989) |
| *Pinus* pollen (1 grain) | genus | Mexico, Chiapas | 16°N 92°W | 14°N 83°W | Late | Langenheim et al. (1967) |
| *Pinus* pollen | genus | Northwestern China, Quidam | 43°N 96°E | 44°N 92°E | Late? | Hsu (1983) |
| *Pinus* pollen | genus | Northwestern China, Northwestern Gansu | 42°N 95°E | 43°N 90°E | Late | Sung (1958) |
| *P. prepityusa* | *Sylvestres* | Western Transcaucasia | 42°N 42°E | 35°N 40°E | Late? | Czeczott (1954) |
| *P. maikopiae* | *Sylvestres/ Contortae* | Eastern Transcaucasia | 40°N 50°E | 35°N 45°E | Late? | Palibin (1935) |

in the Mesozoic. Pines are known from Oligocene deposits that range in North America from the Gulf of Alaska (Wolfe, 1972), British Columbia (Banks et al., 1981), Washington (Underwood & Miller, 1980), Montana (Miller, 1969; Leopold & MacGinite, 1972), Idaho (Axelrod, 1986), Oregon (Wolfe, 1981), Colorado (Leopold & MacGinite, 1972; Schorn & Wolfe, 1989), to a single specimen from Chiapas, Mexico (Langenheim et al., 1967) (Table 4). In Asia, Oligocene deposits are in eastern and western Transcaucasia (Palibin, 1935; Czeczott, 1954), and in northwest China, in the Quidam Basin, and in the Jinguan Basin of western Gansu (Sung, 1958; Hsu, 1983). In Japan, pine was present as a minor component of a few floras (Tanai, 1972). Pine was abundant in the Oligocene strata of Borneo (Muller, 1966). Although some of the pine-bearing deposits were associated with areas of volcanism and mountain-building, others were in lowland and coastal areas where boreotropical flora had flourished in previous epochs.

The climatic deterioration of the early Oligocene was followed by an ameliorating and warming trend during the late Oligocene and into the Miocene. Rainfall, however, stayed moderately low and climatic conditions remained temperate at middle latitudes. The record indicates that pines rose in abundance throughout middle latitudes in North America (Axelrod, 1986), Europe (van der Burgh, 1973; Klaus, 1989), and Asia (Hsu, 1983) in the Miocene; the direct ancestors of many modern pine species can be traced to Miocene pines. The warm conditions of the Miocene supported expanded pine forests at high latitudes, such as Banks Island (78°–80°N, Hills et al., 1974), MacKenzie Delta (72°–85°N, Ritchie, 1984), and Wrangell Mountains, Alaska (68°N, Wolfe, 1969) (Table 5). Pine fossils in low-latitude deposits, such as Veracruz, Mexico (17°N, Graham, 1976) indicate the continued presence of pines in mountainous low latitudes, despite the fact that lowlands in these latitudes were dominated by boreotropical flora.

## Impact of Early Tertiary Climate on Pine Evolution

### Eocene pine refugia

The preceding overview of biogeography provides evidence for the hypothesis that pine distributions shifted latitudinally and that pines expanded and contracted in elevational extent several times from the late Mesozoic to the middle Tertiary. In general, the hypothesis states that pine populations (1) occurred throughout middle latitudes in the Mesozoic, (2) were fragmented and displaced to high and low latitudes and to middle-latitude uplands in the Eocene, and then (3) reappeared widely throughout middle latitudes in the Oligocene and Miocene, where they remained for the rest of the Tertiary.

The Mesozoic origin and spread of pines east and west throughout Laurasia apparently occurred under a warm temperate climate that was equable and had little latitudinal gradation. Early migration and radiation of pines was favored in the Mesozoic not only by climatic conditions, but by the absence at high–middle latitudes of competing angiosperm taxa. Although angiosperms apparently originated about the same time as the pines in the Early Cretaceous (Taylor & Hickey, 1990), their rise to dominance in middle latitudes did not occur until the late Cretaceous (Wolfe & Upchurch, 1986).

The shift in global climates toward warm humid conditions of middle latitudes in the early Tertiary appears to have favored the migration and radiation of angiosperms at the expense of pines. Although pines have broad tolerance of climatic and edaphic conditions, they do not survive or grow well in hot and humid climates (Mirov, 1967). More importantly, in these conditions they are poor competitors with angiosperms in seedling establishment, height growth, and reproduction. Conifers dominate in areas where angiosperm competition is reduced, for example, by fire, cold, or nutrient shortages (Bond, 1989).

Such a situation apparently initiated widespread extirpations of pines over the lowlands at middle latitudes. The remaining areas of suitable pine habitat acted as refugia for pines during the warm, humid periods of the Paleogene.

In general, the fossil evidence indicates three important refugial zones. The circumpolar high-latitude zone originally thought by Mirov to be the cradle of *Pinus* emerges not as a primary Mesozoic center of origin but as an important Eocene refugium. Although many Mesozoic fossils from the polar region that had been identified as pine were later discredited, credible new records, mostly pollen, confirm abundant pine at many high-latitude locations in North America and Eurasia during the warm periods of the Eocene (Table 3). Pines may have been even more widespread during the early Tertiary in polar regions than indicated by the geography of present land masses. Much of the Arctic Sea is shallow, and tectonic evidence suggests that there may have been more land above sea level in polar regions in the early Tertiary than at present (Smith et al., 1981; Wolfe, 1985). Land

connections between North America and Eurasia in the North Atlantic (Tiffney, 1985a, b) would have provided high-latitude corridors for east-west migration of pines during the Eocene (Tiffney, 1985a, b).

The major limiting condition for plant growth poleward now is light. The suggestion that the Earth may have had a lower angle of inclination in the early Tertiary (Wolfe, 1978), which would allow more light at high latitudes, has been discredited (Donn, 1982; McKenna, 1983; Barron, 1984). Alternatively, geophysical and climatic conditions of the early Tertiary may have increased availability of carbon dioxide and permitted plants to photosynthesize under light regimes that were prohibitive under conditions of lower carbon dioxide concentrations that apparently followed the end of the Eocene (Berner et al., 1983; Creber & Chaloner, 1984; Ruddiman & Kutzbach, 1989, 1991; Kerr, 1991).

Low latitudes in North America and Eurasia also appear to have been refugia for pines during the warm humid periods of the Eocene. There is ample evidence that conditions in general were warmer and drier at low latitudes than at middle latitudes in the Eocene. These conditions have been documented for the southeastern United States, Central America, Taiwan (Wolfe, 1975), southern China and southeastern Asia (Guo, 1980; Hsu, 1983), and Borneo (Muller, 1966). During the Paleogene, the southern boundary of Eurasia was the Tethys seaway. Since the Indian subcontinent had not collided with Asia, the area of the present Himalayas marked the Tethys coastline in Asia. Unlike circumpolar regions, the low-latitude dry areas were disjunct and disconnected, even between the southeastern United States and Central America, and refugial populations were unlikely to have been connected by broad migration routes (Wolfe, 1975).

There is less abundant fossil evidence for pines at low latitudes than at high latitudes during the Eocene. There are few early Tertiary plant-bearing deposits in the areas of special interest, such as Mexico, Central America, and the Mediterranean, primarily due to the lack of depositional sediments (Martin & Harrell, 1957; Eguiluz Piedra, 1985). Nevertheless, Eocene pine fossils have been found at low latitudes in southeastern Asia, the southeastern and southwestern United States, and in areas of southeastern Europe that were at low latitudes during the Eocene (Table 3). In Mexico, the single specimen of pine at Chiapas (14°N) from the Oligocene (one of the earliest Tertiary plant records in Mexico), and the abundance of pines in

TABLE 5. Distribution and affinities of select high- and low-latitude fossil pines from Miocene deposits listed in approximate order of age (old to young). Paleocoordinates from Smith et al. (1981).

| Identification | Affinity | Location | Latitude/longitude | | Age (Ma) | Reference |
|---|---|---|---|---|---|---|
| | | | Current | Paleo | | |
| *Pinus* sp. | *Strobi* | Canada, Banks Island | 72°N 122°W | 78°N 92°W | Early | Hills et al. (1974) |
| *Pinus* sp. | genus | Canada | 74°N 122°W | 80°N 87°W | Early | Hills et al. (1974) |
| *Pinus* pollen | genus | MacKenzie Delta/Alaska | 70–80°N 130–150°W | 72–85°N 94–122°W | Early | Ritchie (1984) |
| *Pinus* pollen | genus | Northwestern Borneo | 2°N 110°E | 5°N 110°E | Early | Muller (1966) |
| *Pinus* pollen | genus | Alaska, Nuwok | 70°N 160°W | 78°N 142°W | 22–26 | Wolfe (1972), (1977) |
| *Pinus* pollen | genus | Alaska, Wrangell Mountains | 62°N 140°W | 68°N 122°W | Middle | Wolfe (1969) |
| *Pinus* pollen | genus | Mexico, Veracruz | 17°N 94°W | 17°N 85°W | Middle | Graham (1976) |
| *Pinus* sp. | *Sylvestres* | Spain | not available | | | Klaus (1989) |
| *Pinus* sp. | *Sylvestres* | Greece | not available | | | Klaus (1989) |
| *Pinus* sp. | *Sylvestres* | Yugoslavia | not available | | | Klaus (1989) |
| *Pinus* sp. | *Sylvestres* | Romania | not available | | | Klaus (1989) |

Veracruz (17°N) from the Miocene suggest that pines may have been present in Mexico and Central America earlier (Table 4). Similarly, pines were present in the Oligocene and abundant in Miocene deposits from southern Europe in the region of the Tethys (Palibin, 1935; Czeczott, 1954; Klipper, 1968; van der Burgh, 1973; Klaus, 1989).

Pines were not absent from middle latitudes during the Eocene. Their presence in select fossil deposits from interior western North America testifies to the presence of mid-latitude refugia. Pines in these regions more commonly date to the cool periods of the Eocene. During these times pine populations apparently expanded, whereas during the warm humid periods they contracted into narrow refugial areas where conditions were favorable. During warm humid periods, pines in interior western North America may have been fragmented into small local refugia and, therefore, poorly represented in fossil deposits.

The interior of western North America was anomalous for the Eocene world in having upland areas and centers of volcanism. Several of the pine-bearing deposits occurred at high elevations in Eocene calderas (Thunder Mountain, Idaho; Creede, Colorado), where climates were more temperate than elsewhere at middle latitudes. This region has been documented for angiosperm flora as being one of the first areas at middle latitudes in North America where climatic conditions became temperate during the Paleogene. Widespread volcanism along the cordillera added many cubic meters to the landscape in this region, building a highland that stretched from Arizona to Canada (Leopold & MacGinite, 1972; Wing, 1987; Wolfe, 1987; Ruddiman & Kutzbach, 1991).

Other middle-latitude areas such as eastern Asia may have supported pines during the warm humid periods of the Eocene, although only western North America is known to have had important upland regions. Although the early Tertiary fossil record of eastern Asia is not as complete as in western North America, pines have been found at a few middle-latitude locations in the Eocene. In Japan, the first Tertiary pines date to the last cool period of the Eocene and are not documented for the warm period at the end of the Eocene (Huzioka & Takahashi, 1970; Wolfe, 1985). These Eocene records may represent marginal populations of species that were centered farther north and expanded southward during the cool periods. Boreotropical angiosperms occurred throughout Asia in the warm humid periods of the Eocene, although they do not appear to have extended as far north as in North America (Chaney, 1940; Hsu, 1983).

## SECONDARY CENTERS OF PINE DIVERSITY

The widespread extirpation of pine populations from middle latitudes at the end of the Mesozoic is hypothesized to have led to extinction of many pine species and to have greatly depleted genetic diversity in others. Many Cretaceous fossil pines had combinations of traits not known in extant species and represent lineages that went extinct. Of two closely related pinaceous genera of the Mesozoic, *Pseudoaraucaria* fossils have not been found in rocks younger than the Late Cretaceous, and the youngest *Pityostrobus* fossils date to the early Eocene (Miller, 1976). The disappearance in these two genera of many diverse lineages closely related to *Pinus*, represents major extinctions in the pine family during the early Tertiary.

Despite this depletion of diversity in pines and taxa related to pines, the tectonic events and consequent migrations of the early Tertiary appear to have culminated in the creation of several new centers of pine diversity and the evolution of new pine lineages. This change appears to have been due in large part to increased tectonic activity. Although the period from the Mesozoic through the Paleocene had been relatively quiescent and land elevations were generally low across the continents, by the late Eocene several regions were active tectonically. In subsequent epochs, volcanism and mountain-building became increasingly important locally and globally.

The uplift of new mountain ranges and volcanic activity created environmental heterogeneity. Areas where active mountain-building coincided with Paleogene pine refugia are hypothesized to have become centers of pine radiation. Local climatic diversity was created by elevational differences, and rainshadow and other orographic effects developed. Diversity of soils evolved, with many areas having newly disturbed sites following volcanic activity. Mountain-building created new barriers to migration and gene flow, causing lineages to be fragmented and isolated. All these conditions must have favored divergence and speciation in pines. Conversely, refugial areas that did not undergo major early Tertiary mountain-building, such as the high-latitude zones, were centers from which pines migrated in the Neogene, but did not become important centers of pine speciation.

Although pines expanded and contracted from refugial areas during the fluctuating warm and cool periods of the Eocene, it was the terminal Eocene event that seemed to initiate major migrations out of refugia and to coincide with a time when pines appeared more widespread at middle latitudes. These

migrations provided further opportunities for divergence. As new environments were encountered, genetic isolation may have occurred, and possibilities for genetic drift by founder effects arose, as well as for hybridization with formerly isolated lineages.

## EVOLUTION WITHIN *PINUS* IN RELATION TO EOCENE REFUGIA

By the end of the Paleogene, all subsections of *Pinus*, with the possible exception of *Cembrae*, had evolved (Axelrod, 1986; Millar & Kinloch, 1991). The events of the early Tertiary probably gave rise to at least two subsections, speciation of lineages within several subsections, and the current biogeography of many subsections and groups within several subsections.

The hypothesis that pines were concentrated into refugial regions during the Eocene explains the current bimodal distribution and pattern of diversity of pines at low and high latitudes (see Axelrod, 1986, for maps of pine subsections). In North America three subsections, *Cembroides*, *Leiophyllae*, and *Australes*, appear to have been concentrated in southern refugia during the Eocene and radiated from them subsequently (Axelrod, 1986). Subsections *Cembroides* and *Leiophyllae* seem to have been limited to western North America and Central American refugia whereas *Australes* may have had refugial areas with a broader southern distribution, including the Gulf Coast (Tables 3, 4). The current distribution of *Australes* in both the southeastern United States and in Central America/Caribbea suggests that *Australes* may have had refugia in both regions. Although not identifiable to subsection, the abundant pine fossils of the Eocene from southern Alabama (Table 3) are from a site that is within the range of several extant species of *Australes*. Small genetic distances between taxa of *Australes* versus *Leiophyllae* (Strauss & Doerksen, 1991) suggest that these subsections were in contact or did not diverge from each other until after the Mesozoic.

Four subsections in North America appear to have been fragmented by Eocene events into several refugial regions. A division into northern and southern refugia in subsection *Sylvestres* is indicated by the extant lineages of *P. resinosa* (40°–52°N) and *P. cubensis* (restricted to Cuba, 22°N). Eocene fossils with affinities to *Sylvestres* that support a northern refugium have been found in British Columbia and northern Washington (Table 3).

Subsection *Contortae* similarly seems to have been divided into northern and southern refugia: the lineages leading to *P. contorta* and *P. banksiana* clearly had northern origins and boreal adaptations, whereas those leading to *P. clausa* and *P. virginiana* had southeastern affinities. Eocene fossils with affinities to *Contortae* have been found in northern Washington, and Oligocene fossils in British Columbia, corroborating a northern refugium (Tables 3, 4).

Subsection *Ponderosae* also may have had both northern and southern refugia. There are 10–17 species endemic or nearly endemic to Mexico and Central America, whereas wide-ranging *Pinus ponderosa* has a northern distribution and northern ecological affinities in its habitat preference and vegetation associates. Early Tertiary pines most closely allied to *Ponderosae* have been found in British Columbia (Eocene, Table 3), northern Washington, and Montana (Oligocene, Table 4). Lineages of *Ponderosae* may have been concentrated also in Rocky Mountain refugia, as suggested by Oligocene fossils from Colorado with affinities to this subsection (Table 3). A recent re-evaluation of evolutionary patterns in *Ponderosae* also indicates northern and southern division in the subsection (Lauria, 1991). *Pinus ponderosa* is considered to originate in northern latitudes, while other distinct phylads had southern origins in Mexico and Central America.

Subsection *Strobi* has northern and southern lineages in North America. Ancestral lineages of *Pinus monticola* and *P. strobus* would have migrated from northern refugia, and those of *P. strobiformis*, *P. ayacahuite*, and *P. chiapensis* (Martinez) Andresen (distinct from *P. strobus*, of which it was once classed as a variety; Andresen, 1964, 1966) would have migrated from southern refugia. Northern refugia are corroborated by Eocene fossil pines allied to subsection *Strobi* from British Columbia (Table 3). Lineages of subsection *Strobi* may also have been fragmented into middle-latitude refugia in the Rocky Mountain region, represented currently by *P. flexilis* and possibly *P. strobiformis*, and by Oligocene fossils from Idaho and Colorado (Table 4).

The small subsection *Balfourianae* is an ancient lineage (Kossack, 1989; Strauss & Doerksen, 1991; Millar & Kinloch, 1991) that appears to have been entirely concentrated in middle-latitude Rocky Mountain refugia during the early Tertiary. Present distribution of the three closely related species is in the Rocky Mountain/Great Basin/Sierra–Cascades Ranges of the western United States between 35°N and 41°N latitude. Early Tertiary fossils with probable affinities to this subsection were found in Idaho (Eocene) and Colorado (Oligocene) (Tables 3, 4).

In Eurasia, sequences of conifer-bearing deposits from the early Tertiary are not as widely distributed as in North America, but evidence for pine evolution in relation to refugia exists. Three ancient subsections, *Canarienses*, *Pineae*, and *Krempfiani*, have extant species restricted to regions that were along the Tethys seaway. Fossil evidence exists for a Tethys refugial area of pines in southeast Asia, in the region where *P. krempfii* now occurs. Pine was recorded in abundance throughout early Tertiary strata and in coastal southeast China and in northwest Borneo (Tables 3, 4). Other fossil floras for southeast Asia include temperate taxa, suggesting that pines would have found favorable habitats.

In western Europe, the boreotropical angiosperm flora was recorded abundantly from 45°N to 56°N (Chaney, 1940). Although there are no fossil records from currently low latitudes in Europe, pine fossils are known from areas of southeast Europe that were along the Tethys seaway (Chiguriaeva, 1952; Mirov, 1967). Furthermore, there is indication of dry zones in the middle Eocene along the European and north African Tethys, indirectly supporting the occurrence of pines there (Parrish et al., 1982; Parrish, 1987). Fossil pines allied to *Canariensis* and *Pineae* were widespread along the Tethys seaway in western Europe during the Miocene (reviewed in Klaus, 1989), suggesting more widespread distributions for both subsections in this region in the early Tertiary.

As in North America, in Eurasia several subsections appear to have been divided by Eocene events into northern and southern refugia. In *Sylvestres*, lineages represented by extant *P. sylvestris* most likely migrated from northern refugia. Eocene pine fossils from high latitudes in western Siberia allied to *Sylvestres* corroborate a northern refugium in Eurasia. The remaining 14 extant species in *Sylvestres*, excluding *P. densiflora*, and *P. thunbergiana*, and possibly *P. yunnanensis*, represent lineages from southern refugia. Although few Eocene deposits from southern Europe are plant-bearing, abundant fossils allied to *Sylvestres* are known from Oligocene and Miocene deposits in the Tethys region (Table 5; Palibin, 1935; Czeczott, 1954; Klipper, 1968; van der Burgh, 1973; Klaus, 1989). The exceptional three species may represent lineages from middle-latitude refugia, as documented by fossil pollen of unknown affinity from the Eocene and Oligocene of Japan and northern China (Tables 3, 4). Subsection *Gerardianae* may have been divided between a southern Tethys refugium, as represented by extant *P. gerardiana*, and a middle-latitude refugium in northern China, as represented by extant *P. bungeana*, and by early Tertiary deposits containing pine pollen in China (Tables 3, 4).

Refugia for subsection *Strobi* in Eurasia were mostly along the Tethys. Of the eight extant Eurasian species in the subsection, only *P. parviflora* seems clearly allied to lineages derived from more northerly refugia. The remaining seven modern species are all distributed along the former Tethys region. No early Tertiary fossils from Eurasia have been specifically allied with subsection *Strobi*, although Miocene fossils of the subsection testify to their presence in that region (Klipper, 1968).

The consequence of certain Eocene refugia becoming secondary centers of pine diversity is best described for Mexico and Central America. Although parts of the Mexican and Central American isthmuses were transiently under water during the Mesozoic (Kellum, 1944; Eguiluz Piedra, 1985), they were elevated during the Eocene and later Tertiary. Tectonic activity was especially great in Mexico during the late Eocene and Oligocene/Miocene. Tertiary volcanic activity significantly reshaped the Sierra Madre Occidental and created the Sierra Madre Oriental and the Transversal Neovolcanic Axis. Uplift in the early Eocene rebuilt almost the entire ranges of the Sierra Madre del Sur and Sierra Madre de Chiapas (Eguiluz Piedra, 1985).

Mexico and Central America are home to as many as 83 extant taxa of pines, including 48 species, 21 varieties, and 14 forms (Eguiluz Piedra, 1985). Within many subsections, extensive radiation and speciation are ongoing, which has been attributed to active mountain-building that began in the Eocene (Equiluz Piedra, 1985; Axelrod, 1986; Karamangala & Nickrent, 1989; Lauria, 1991). Active radiation is evidenced by closely related species clusters, with subsections *Ponderosae* and *Cembroides* the best examples. There are 10–17 species of *Ponderosae* (Eguiluz Piedra, 1985) endemic to Mexico and Central America and 10–16 species in *Cembroides* (Zavarin, 1988). The difficulty of separating the taxa of *Cembroides*, implying close genetic relationship, has led some botanists to the conclusion that *Cembroides* is a young subsection. Phylogenies based on DNA-sequence divergence indicate, however, that section *Parrya*, including subsection *Cembroides*, is ancient (Kossack, 1989; Strauss & Doerksen, 1991). Ancestral *Cembroides* lineages would have been concentrated in Mexican/Central American refugia during the early Tertiary, and the major pulse of radiations now occurring in the subsection may have begun in the early Tertiary.

Two subsections may have originated in Mexican/Central American refugia (Axelrod, 1980, 1986). Unlike other subsections, *Oocarpae* and *Sabinianae* have no Mesozoic fossil record and are not clearly documented until the Miocene. On the basis of specialized and apparently derived morphological adaptations (Shaw, 1914, 1924; Little & Critchfield, 1969; Klaus, 1980; van der Burgh, 1984), these subsections have long been considered to have originated recently. Phylogenetic analysis of DNA divergence also confirms their relative youth, especially of *Oocarpae* (Strauss & Doerksen, 1991). Using fossil and floristic evidence, Axelrod (1980) traced the origins of the northern (California/Baja California) elements of *Oocarpae* to mainland Mexico/Central America prior to the Miocene. The northern lineages appear to have diverged by the time they reached California (Millar et al., 1988), indicating that the radiation events occurred farther south in the early Tertiary. Although the systematic coherence of the extant Latin American taxa of *Oocarpae* remains uncertain, genetic relationships of some Latin American species link *Oocarpae* with *Australes* and *Ponderosae* (Critchfield, 1967), both of which have Mesozoic fossil records, appear to have had Mexican/Central American Paleogene refugia, and may have been ancestral to *Oocarpae*.

Subsection *Sabinianae* has a limited fossil record consisting of a single taxon allied to *P. sabiniana* and confined to southern California (Axelrod, 1986). Fossils are known only from the late Miocene through Quaternary, and Axelrod (1981) traced the origin of the extant species to Mexican species of *Ponderosae*. Genetic relationships of extant taxa link *Sabinianae* with *Ponderosae* on the basis of terpene affinities (Zavarin et al., 1967) and crossing evidence (Critchfield, 1966; Conkle & Critchfield, 1988). Together this evidence points to a Mexican/Central American origin of *Sabinianae* from early Tertiary *Ponderosae* lines.

## Pleistocene Versus Eocene Impacts

In this paper I document that tectonic, climatic, and biogeographic events of the Eocene had a major impact on pine distributions and evolution. The question may arise whether the effects of the Eocene were so confounded by subsequent events of the Tertiary and especially the Quaternary as to be indecipherable. I will address only the Pleistocene, since its potential was probably the greatest.

The Pleistocene was a time of profound change unprecedented in the history of the Earth. In some ways the Pleistocene was analogous to the Eocene. The Pleistocene was also an epoch with fluctuating climates, but the deviation from temperate climates in the Pleistocene was toward glacial conditions, whereas in the Eocene it was toward tropical episodes. The amplitude in average temperature between glacial and interglacial periods of the Pleistocene (5°–10°C, Bowen, 1979) was about the same as estimated for the cool and warm periods of the Eocene. The Pleistocene differed in lasting only 2 million years (cf. 20 million years for the Eocene), in having many more cycles (16–18, Bowen, 1979), and in having alternating periods of unequal duration with glacials longer than interglacials.

The events of the Pleistocene had enormous effects on vegetation, including pines. In northern latitudes, pine distributions were displaced by continental ice sheets (e.g., *Pinus contorta/P. banksiana*, Critchfield, 1985); in mountainous regions elsewhere, species migrated up or down in elevation (Miki, 1957; Van Devender & Spaulding, 1979). Along coasts and in other lowlands, pine populations shifted north and south in response to the climate cycles (e.g., *Oocarpae*, Axelrod, 1980; Millar, 1983). Concomitant to the shifts in distribution of pines were major changes in the genetic structure of species. The flux of population expansion and contraction, coupled with drastically changing selection regimes, affected the structure of genetic variation within species and allowed some species to hybridize (Critchfield, 1984, 1985; Kinloch et al., 1986; Millar, 1989).

In general, however, the Pleistocene does not appear to have completely reshuffled the genus in the way the Eocene did, and many of the Tertiary patterns and the evolutionary events that date to that period have been maintained. Notwithstanding the existence of local refugia, Pleistocene events primarily affected *Pinus* in a gradient from north to south, with the effect that species and populations shifted south then north (or down then up in elevation) following the cycle of the glacial and interglacial periods.

The impact of the Eocene, by contrast, was greatest in the latitudinal center of the genus and had the effect of dissecting the genus and concentrating pines into widely disjunct regions. Furthermore, during the early Tertiary, and unlike the Pleistocene, almost no upland regions (except in interior western North America) could offer local refuge from unfavorable climates. Whereas many pine species appear to have gone extinct in the early Tertiary, no pine extinctions in North America are attributed to the Pleistocene (Critchfield,

1984), although western Europe suffered a significant impoverishment of pine flora (Klipper, 1968). Some speciation, for example, in *Balfourianae*, *Cembroides*, and *Oocarpae*, seems to have been triggered by the Pleistocene, but no major new trends have emerged.

Insufficient time has elapsed since the close of the Pleistocene for its full impact to be felt on evolution in *Pinus*. Patterns initiated by the Pleistocene appear minor compared to the effects of the Eocene and are insufficient to erase the evolutionary impacts of the early Tertiary. Thus, many of the major evolutionary patterns of the early Tertiary can still be traced in the biogeography and relationships of extant pines.

## Validation of the Hypothesis

The arguments developed in this paper result in a working hypothesis about the effect of the Eocene on pine evolution. The hypothesis is a reconstruction of pine history based on available information from the fossil record, climatic and tectonic evidence, and biogeographic record of angiosperms and conifers. Many gaps in information exist that, if filled, would corroborate or negate this hypothesis. These gaps fall into several categories. Expanded fossil records are urgently needed, especially in regions hypothesized as Eocene pine refugia that currently have meager fossil documentation. These include Paleogene records for Central America and Mexico, low latitudes along the European Tethys, and high latitudes in eastern Asia. Technologies that allow more accurate identification of fossil affinities for macro- and especially micro-fossils at intrageneric levels would help in tracking the biogeography and evolution of these groups. These technologies need to be applied to published fossil floras, with revised taxonomic lists. Certain pine lineages have especially meager fossil records, including Cretaceous records of sections *Parrya*, especially *Gerardianae* and *Balfourianae*, and Cretaceous/early Tertiary records of section *Pinea*. Accurate dating of fossils and correlation with paleoclimatic and paleogeological events will also help to track the fine scale paths of these pines. Finally, existing and emerging genetic and molecular technologies should be applied to estimate genetic distances and divergence times among subgeneric groups. Such genetic techniques will allow tests of the hypothesized times of geographic isolation.

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# PLANT LIFE-FORMS AND BIOGEOGRAPHIC RELATIONS OF THE FLORA OF LAGUNILLAS (30°S) IN THE FOG-FREE PACIFIC COASTAL DESERT[1]

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## Abstract

The coastal desert of north-central Chile supports a rich but poorly known flora. Here, we document the importance of the annual and perennial habits in the flora of Lagunillas (30°S), at the southern transition from the desert to the mediterranean climate region, and discuss the origin of the desert flora by examining the geographic distribution of the taxa at the level of genus. The distribution was used to assign the species to six biogeographic elements. Annual plants represent 41% of the total flora (191 species) and are the most important life form. Excluding non-native weeds, however, decreases the importance of annuals to 33%. This value is higher than that for high-altitude deserts, but lower than for most other, less-equitable, lowland deserts both in North America and eastern Asia. Shrubs, geophytes, and other perennial herbs comprise 33%, 12%, and 21% of the native flora, respectively. The Cosmopolitan element, including weed species, accounts for 41% of the coastal desert flora. South American taxa include desert endemics (13%), Andean (12%), and Tropical American (10%) species. A large proportion (15%) of the taxa, especially shrubs, have disjunct distributions in the arid regions of North and South America. Results suggest that the present coastal desert flora derives primarily from recently diversified coastal desert and Andean taxa, most of them endemic to these areas, and secondarily from cosmopolitan weeds. The presence of a number of amphitropic xerophytes lends support to the hypothesis that arid habitats were continuous through the lowland tropics during the Glacial period.

The Pacific coastal desert of South America ranges from southern Ecuador at ca. 5°S, to about 32°S in north-central Chile (Rauh, 1985). Three major climatic and vegetational zones have been recognized within this extensive geographic region (Rauh, 1985): the narrow "tree-desert" zone of Ecuador and northern Peru, dominated by savannas and drought-deciduous forests; the "fog-loma" desert of Peru and northern Chile, with isolated patches of perennial and ephemeral vegetation maintained by permanent fog on the heights of the coastal range; and the fog-free northern Chilean coastal desert, with a predominantly ephemeral vegetation that develops on lowland areas in response to irregular rainfall events. The modern climate of the Pacific coastal desert is subjected to the desiccating influence of the Humboldt cold current, which also produces a negative thermal anomaly, resulting in temperatures 3–5°C lower than expected for the corresponding latitude, as well as highly uniform temperatures throughout the region (Ochsenius, 1982).

Arid environments developed very recently in South America (Ochsenius, 1982; Arroyo et al., 1988), in close association with geoclimatic events such as the Andean orogenesis and the onset of the Antarctic glaciation, both of which became more intense during Pleistocene–Holocene times. Tertiary climates were generally warmer and wetter than the present (Solbrig, 1976), and tropical forests covered most of the mountainless South American landscape. Climatic changes began in the mid-Eocene with a gradual decrease in temperature and an increase in the drying effect of the Andean range. Because of the rapid inception of the arid climate (Simpson, 1975; Ochsenius, 1982), the Pacific coastal desert provides a unique scenario to examine how plant and animal communities become modified by sudden environmental changes (e.g., Arroyo et al., 1988).

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Although partial floristic accounts are available for certain areas, especially in the "fog-loma" region of southern Peru and northern Chile (e.g., Johnston, 1929; Ellenberg, 1959; Rundel & Mahu, 1976; Péfaur, 1982; Torres & López-Ocaña, 1982; Dillon, 1985; Rundel et al., 1991), complete systematic surveys of the local floral or fauna and their relation to other world biotas are lacking for many areas in the fog-free southern Atacama desert. This information can be relevant for refining and enhancing current paleoecological, geological, and climatic models about the Pacific coastal desert. In this paper we present the results of a survey of the vascular flora of Lagunillas (30°S), located at the southern margin of the fog-free coastal desert of north-central Chile (Fig. 1). Our goals were to assess the importance of the annual and perennial habits in the flora of Lagunillas in relation to other deserts of the world, and to examine the biogeographic relationships of the taxa in order to advance our understanding of the origins and history of the coastal desert flora.

## Study Site

Fieldwork was conducted at Lagunillas (Fig. 1), 15 km south of Coquimbo (30°06′S, 71°21′W), Chile, a field station managed by the Universidad de La Serena. Floral surveys encompassed approximately 25 km² of a gently sloping, extensive coastal terrace, traversed from east to west by an intermittent ravine up to 10 m deep and 10–20 m wide, which remains dry during most of the year. Extensive coastal terraces are a frequent feature of the coastal desert landscape between 27 and 30°S (Börgel, 1983). Altitude ranged from sea level up to 400 m on the summits of the nearby coastal hills. The terrace was covered by modern and fossil dunes, deposited over a calcareous hard-pan (caliche) layer, which extends throughout the area. The calcareous hard-pan is found at variable depths, surfacing in some places, especially on the slopes of the ravine. Further inland, closer to the coastal hills, alluvial deposits become more important, and a rocky substrate prevails on the surrounding hillsides.

The regional climate is semiarid with an average annual rainfall of 130 mm (di Castri & Hajek, 1976). Eight years of climatic records for Faro Punta Tortuga in Coquimbo (30°S) (E. Hajek, pers. comm.) indicate that annual precipitation is highly variable, with a maximum of 200 mm and a minimum of 30 mm. Records for 15 years from La Serena (29°54′S) indicate yearly totals varying between 0 and 177.5 mm (Muñoz, 1985). Rains fall mainly between April and July (winter). Air temperature rarely exceeds 22°C or falls below 10°C. For La Serena, the annual average is 14.7°C, and the mean minimum and maximum temperatures are 11.7°C and 18.4°C, respectively (Fuenzalida, 1965). Due to the accentuated influence of the ocean, air humidity remains over 80% during most of the year.

The vegetation is physiognomically dominated by evergreen and summer-dormant shrubs, except for a few months after the rains when herbs become abundant. The most common shrub species are *Encelia tomentosa*, *Haplopappus cerberoanus*, and *Flourensia thurifera*. Average shrub cover during the dry season varies between 8 and 25% (J. Gutiérrez, unpublished data). After the rainy season, plant cover increases up to 90% due to the growth of shrubs and the development of a dense cover of annuals and geophytes (Armesto, Vidiella & Gutiérrez, in press). Human impact through dry farming, and cattle and goat grazing has been important in this area as in most of the coastal desert. Before 1962, portions of the study area were cultivated in wet years mainly for wheat and potatoes, and they have been intermittently grazed since then. Nevertheless, the flora is representative of that of other less-disturbed areas of the coastal desert (unpublished data of the authors).

## Methods

Collections of plants used in this survey were conducted in Lagunillas during the growing seasons (September–December) of 1987, 1988, and 1989. No previous collections for the area were available. The number of species present in the area varies from year to year depending on the amount of rainfall. In years with low rainfall (20 mm or less), plant cover is composed mainly of shrubs and exotic weed species (Armesto, Vidiella & Gutiérrez, in press). The period of study included two years of abundant rainfall (1987: 168 mm; 1989: 80 mm), and hence we are reasonably certain that all plants potentially growing in the area have been collected. Voucher specimens of all the species collected were stored at the Herbarium of the Universidad de La Serena (ULS). Nomenclature of species follows Marticorena & Quezada (1985), except for the Nolanaceae, which follows Mesa (1981). Plants were classified by life form (annual herbs, perennial herbs, geophytes, and shrubs) according to field observations and the literature. For each genus, the number of species present in Chile (Marticorena

& Quezada, 1985), and the estimated total number of species known from all the world (Mabberley, 1987) were also compiled.

According to the modern geographic distributions of the genera, obtained primarily from Willis (1985) and Mabberley (1987), we assigned the species to the following biogeographic elements: (1) Cosmopolitan: species of genera distributed in several continents, both in temperate and tropical regions; (2) Pantropical: genera distributed within the tropics of the Old and New World; (3) Tropical American: genera primarily distributed in the lowland tropics of Central and South America; (4) Amphitropical (sensu Raven, 1963): genera occur primarily in warm deserts of North and South America, but are absent from the tropical regions in between; (5) Andean: genera mostly restricted to the tropical and/or temperate Andes of South America; and (6) Endemic: genera confined to the Pacific coastal desert of northern Chile and southern Peru.

For some genera, assignments were made based on systematic revisions. For example, the genus *Calandrinia* occurs in desert regions of North and South America and Australia. However, current evidence indicates that the genus spread and diversified in the Andes of South America (Kelley, 1973). Hence we assigned the species of *Calandrinia* to the Andean element. Although the genus *Fuchsia* has a broad distribution from North to South America, in addition to New Zealand and Tahiti, *Fuchsia lycioides* is the only member of the section *Kierschlegeria* that is restricted to the coast of north-central Chile (Berry, 1982) and related to other South American sections. We assigned this species to the Tropical American element. The genus *Tristerix* was assigned to the Andean element based on the work of Kuijt (1988). Finally, four genera (*Astephanus*, *Lastarriaea*, *Mesembryanthemum*, *Muehlebechia*) had unknown distributions, or their distribution did not fit the definitions given above.

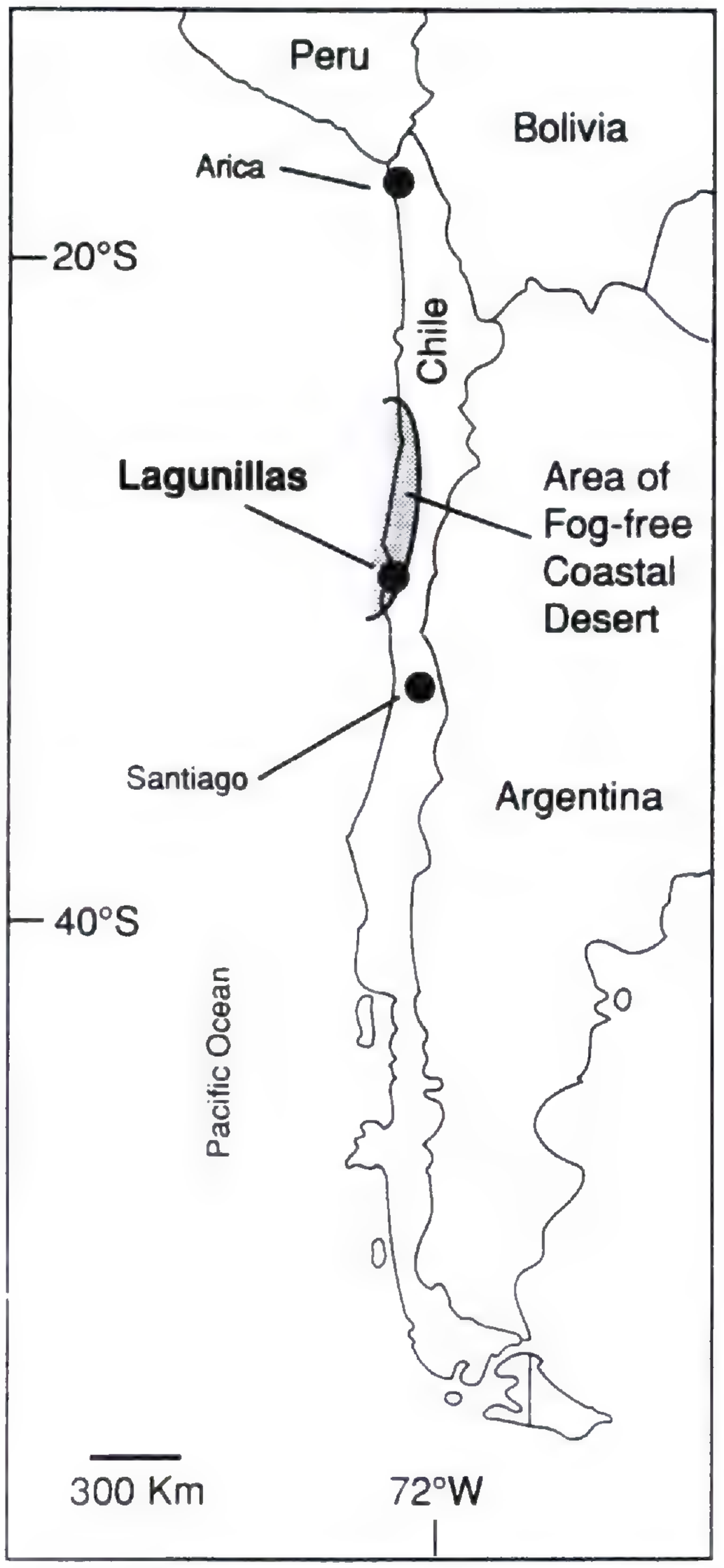


FIGURE 1. Location of Lagunillas, the study site in north-central Chile. The stippled area marks the approximate extent of the fog-free Pacific coastal desert.

## RESULTS

### FLORISTICS

A total of 191 vascular plant species, belonging to 61 families, have been collected within an area of about 25 km² in Lagunillas (Table 1). The families with the highest number of species in the flora are Compositae, Gramineae, Boraginaceae, Liliaceae, Papilionaceae, Onagraceae, and Amaryllidaceae (Table 2). Compared to the composition of the flora of a high-altitude desert in northern Chile (Arroyo et al., 1982), the coastal desert is characterized by a lower diversity of Gramineae and by the presence of bulbous monocots (Liliaceae, Amaryllidaceae). The relevance of Liliaceae and Amaryllidaceae in the coastal desert is also contrasted with the lower relative frequency of these families in the flora of Chile (Table 2). Onagraceae and Boraginaceae also seem to be better represented in the coastal desert than in the Chilean flora or in the high-Andean desert flora (Table 2).

TABLE 1. Species collected in the area of Lagunillas in the Chilean coastal desert, and their assignments to biogeographic elements based on the distribution of the genera. See text for definition of elements. * = Introduced species.

| Species | Family | Number of species Chile | Number of species total | Biogeographic element | Life form |
|---|---|---|---|---|---|
| *Acacia caven* (Mol.) Mol. | Mimosaceae | 8 | 1,200 | PANTROP | Shrub |
| *Adesmia filifolia* Clos | Papilionaceae | 140 | 230 | ANDEAN | Annual |
| *Adesmia microphylla* H. et A. | Papilionaceae | 140 | 230 | ANDEAN | Shrub |
| *Adesmia tenella* H. et A. | Papilionaceae | 140 | 230 | ANDEAN | Annual |
| *Alonsoa meridionalis* (L. f.) O. K. | Schrophulariaceae | 1 | 6 | TROP AM | Perennial |
| *Alstroemeria gayana* Phil. | Amaryllidaceae | 29 | 50 | TROP AM | Geophyte |
| *Alstroemeria kingii* Phil. | Amaryllidaceae | 29 | 50 | TROP AM | Geophyte |
| *Alstroemeria sierrae* Muñoz | Amaryllidaceae | 29 | 50 | TROP AM | Geophyte |
| *Amblyopappus pusillus* H. et A. | Compositae | 1 | 1 | AMPHI | Annual |
| *Ambrosia chamissonis* (Less.) Greene | Compositae | 4 | 24 | COSM | Perennial |
| *Amsinckia calycina* (Moris) Chater | Boraginaceae | 2 | 50 | AMPHI | Annual |
| *Ancrumia cuspidata* Harv. ex Baker | Liliaceae | 1 | 1 | ENDEM | Geophyte |
| *Anisomeria littoralis* (P. et E.) Moq. | Phytolaccaceae | 2 | 2 | ENDEM | Shrub |
| *Argylia radiata* (L.) D. Don | Bignoniaceae | 11 | 12 | ANDEAN | Annual |
| *Argythamnia berterana* (Schlecht.) Muell.-Arg. | Euphorbiaceae | 4 | 17 | AMPHI | Shrub |
| *Aristolochia bridgesii* (Klotzsch) Duchart. | Aristolochiaceae | 2 | 300 | PANTROP | Perennial |
| *Aristolochia chilensis* Bridges ex Lindl. | Aristolochiaceae | 2 | 300 | PANTROP | Perennial |
| *Astephanus geminiflorus* Decne. | Asclepiadaceae | 1 | 30 | (1) | Perennial |
| *Astragalus amatus* Clos | Papilionaceae | 46 | 2,000 | COSM | Annual |
| *Atriplex repanda* Phil. | Chenopodiaceae | 25 | 100 | COSM | Shrub |
| *Baccharis* sp. | Compositae | 42 | 350 | AMPHI | Shrub |
| *Baccharis linearis* (R. et P.) Pers. | Compositae | 42 | 350 | AMPHI | Shrub |
| *Bahia ambrosioides* Lag. | Compositae | 1 | 12 | AMPHI | Shrub |
| *Berberis glomerata* H. et A. | Berberidaceae | 50 | 450 | COSM | Shrub |
| *Bidens pilosa* L. | Compositae | 42 | 233 | COSM* | Shrub |
| *Bridgesia incisifolia* Bert. ex Cambess. | Sapindaceae | 1 | 1 | ENDEM | Shrub |
| *Bromus berterianus* Colla | Gramineae | 22 | 50 | COSM | Annual |
| *Bromus* sp. | Gramineae | 22 | 50 | COSM | Annual |
| *Caesalpinia angulata* (H. et A.) Baillon | Caesalpiniaceae | 5 | 100 | PANTROP | Shrub |
| *Calandrinia* sp. | Portulacaceae | 70 | 150 | ANDEAN | Annual |
| *Calandrinia grandiflora* Lindl. | Portulacaceae | 70 | 150 | ANDEAN | Perennial |
| *Calceolaria picta* Phil. | Schrophulariaceae | 86 | 300 | PANTROP | Annual |
| *Camassia biflora* (R. et P.) Coc. | Liliaceae | 1 | 6 | AMPHI | Geophyte |

TABLE 1. Continued.

| Species | Family | Number of species Chile | Number of species total | Biogeographic element | Life form |
|---|---|---|---|---|---|
| *Camissonia dentata* (Cav.) Reiche | Onagraceae | 1 | 55 | AMPHI | Annual |
| *Cardionema ramosissimum* (Weinm.) Nels. et Macbr. | Caryophyllaceae | 3 | 6 | AMPHI | Perennial |
| *Centaurea chilensis* H. et A. | Compositae | 11 | 450 | COSM | Shrub |
| *Cestrum parqui* L'Herit. | Solanaceae | 1 | 175 | TROP AM | Shrub |
| *Chaetanthera limbata* (D. Don) Less. | Compositae | 36 | 41 | ANDEAN | Annual |
| *Chaetanthera linearis* Poepp. ex Less. | Compositae | 36 | 41 | ANDEAN | Annual |
| *Chenopodium ambrosioides* L. | Chenopodiaceae | 24 | 150 | COSM | Annual |
| *Chenopodium murale* L. | Chenopodiaceae | 24 | 150 | COSM* | Annual |
| *Chenopodium album* L. | Chenopodiaceae | 24 | 150 | COSM* | Annual |
| *Chorizanthe kingii* Phil. | Polygonaceae | 25 | 50 | AMPHI | Perennial |
| *Chuquiraga aicularis* D. Don | Compositae | 6 | 25 | ANDEAN | Shrub |
| *Clarkia tenella* (Cav.) Lewis et Lewis | Onagraceae | 1 | 36 | AMPHI | Annual |
| *Conanthera campanulata* (D. Don) Lindl. | Tecophilaceae | 6 | 6 | ENDEM | Geophyte |
| *Convolvulus chilensis* Pers. | Convolvulaceae | 6 | 250 | COSM | Perennial |
| *Cordia decandra* H. et A. | Boraginaceae | 1 | 250 | PANTROP | Shrub |
| *Corrigiola* sp. | Caryophyllaceae | 3 | 10 | COSM | Perennial |
| *Cotula coronopifolia* L. | Compositae | 4 | 80 | COSM* | Perennial |
| *Crassula closiana* (Gay) Reiche | Crassulaceae | 7 | 300 | COSM | Annual |
| *Cristaria glaucophylla* Cav. | Malvaceae | 62 | ? | ENDEM | Perennial |
| *Cristesion murinum* (L.) Love | Gramineae | 14 | ? | COSM* | Annual |
| *Cryptantha dolichophylla* (Phil.) Reiche | Boraginaceae | 40 | 40 | COSM | Annual |
| *Cryptantha glomerata* Lehm. | Boraginaceae | 40 | 40 | COSM | Annual |
| *Cryptantha glomerulifera* (Phil.) Johnst. | Boraginaceae | 40 | 40 | COSM | Annual |
| *Cuscuta chilensis* Ker-Gawl. | Cuscutaceae | 10 | 145 | COSM | Annual |
| *Cynanchum boerhaviifolium* H. et A. | Asclepiadaceae | 9 | 100 | COSM | Perennial |
| *Cynanchum pachyphyllum* (Decne.) Schum. | Asclepiadaceae | 9 | 100 | COSM | Perennial |
| *Descurainia cumingiana* (Fisch. et Mey.) Prantl | Cruciferae | 15 | 55 | COSM | Annual |
| *Dichondra* sp. | Convolvulaceae | 1 | 9 | PANTROP | Perennial |
| *Dioscorea hemifusa* Poepp. | Dioscoreaceae | 42 | 600 | PANTROP | Perennial |
| *Encelia canenscens* Lam. | Compositae | 1 | 15 | AMPHI | Shrub |
| *Ephedra andina* Poepp. ex C. A. Mey. | Ephedraceae | 7 | 40 | COSM | Shrub |
| *Erigeron* sp. | Compositae | 17 | 200 | COSM | Annual |
| *Erodium cicutarium* (L.) L'Herit. ex Aiton | Geraniaceae | 4 | 60 | COSM* | Annual |
| *Erodium malacoides* (L.) L'Herit. ex Aiton | Geraniaceae | 4 | 60 | COSM* | Annual |

TABLE 1. Continued.

| Species | Family | Number of species Chile | Number of species total | Biogeographic element | Life form |
|---|---|---|---|---|---|
| *Erodium moschatum* (L.) L'Herit. ex Aiton | Geraniaceae | 4 | 60 | COSM* | Annual |
| *Eryngium coquimbanum* Phil. ex Urban | Umbelliferae | 16 | 230 | COSM | Annual |
| *Eupatorium glechonophyllum* Less. | Compositae | 2 | 38 | COSM | Shrub |
| *Eupatorium salvia* Colla | Compositae | 2 | 38 | COSM | Shrub |
| *Euphorbia elquiensis* Phil. | Euphorbiaceae | 28 | 1,600 | COSM | Annual |
| *Euphorbia peplus* L. | Euphorbiaceae | 28 | 1,600 | COSM* | Annual |
| *Fagonia chilensis* H. et A. | Zygophyllaceae | 2 | 30 | COSM | Shrub |
| *Frankenia* sp. | Frankeniaceae | 4 | 25 | COSM | Perennial |
| *Fuchsia lycioides* Andr. | Onagraceae | 2 | 100 | TROP AM | Shrub |
| *Fumaria* sp. | Fumariaceae | 4 | 55 | COSM* | Perennial |
| *Galium aparine* L. | Rubiaceae | 22 | 400 | COSM* | Annual |
| *Gilia valdiviensis* Griseb. | Polemoniaceae | 4 | 25 | AMPHI | Annual |
| *Gilliesia graminea* Lindl. | Liliaceae | 4 | 44 | ENDEM | Geophyte |
| *Glandularia sulphurea* (D. Don) Schnack et Covas | Verbenaceae | 6 | 250 | COSM | Perennial |
| *Gnaphalium heterophyllum* Phil. | Compositae | 31 | 150 | COSM | Perennial |
| *Gnaphalium viravira* Mol. | Compositae | 31 | 150 | COSM | Perennial |
| *Gutierrezia resinosa* (H. et A.) Blake | Compositae | 6 | 19 | AMPHI | Shrub |
| *Gymnophyton robustum* Clos | Umbelliferae | 5 | 6 | ANDEAN | Shrub |
| *Haplopappus hirtellus* Phil. | Compositae | 61 | 160 | AMPHI | Shrub |
| *Haplopappus parvifolius* (DC.) A. Gray | Compositae | 61 | 160 | AMPHI | Shrub |
| *Haplopappus cerberoanus* (Remy) Reiche | Compositae | 61 | 160 | AMPHI | Shrub |
| *Helenium aromaticum* (Hook.) Bailey | Compositae | 7 | 40 | AMPHI | Annual |
| *Helenium urmenetae* (Phil.) Cabr. | Compositae | 7 | 40 | AMPHI | Annual |
| *Heliotropium stenophyllum* H. et A. | Boraginaceae | 26 | 250 | COSM | Shrub |
| *Herniaria cinerea* DC. | Caryophyllaceae | 1 | 20 | COSM* | Annual |
| *Hippeastrum bagnoldii* (Herb.) Baker | Amaryllidaceae | 28 | 76 | TROP AM | Geophyte |
| *Hippeastrum pratense* (Poepp.) Baker | Amaryllidaceae | 28 | 76 | TROP AM | Geophyte |
| *Homalocarpus bowlesioides* H. et A. | Umbelliferae | 5 | 5 | ENDEM | Annual |
| *Hypochaeris minima* Desf. | Compositae | 36 | 50 | COSM | Annual |
| *Junellia selaginoides* (Kunth) Mold. | Verbenaceae | 28 | 57 | ANDEAN | Shrub |
| *Koeleria* sp. | Gramineae | 3 | 25 | COSM | Annual |
| *Krameria cistoidea* H. et A. | Krameriaceae | 2 | 15 | AMPHI | Shrub |
| *Lamarckia aurea* (L.) Moench | Gramineae | 1 | 1 | COSM* | Annual |
| *Lastarriaea chilensis* Remy | Polygonaceae | 1 | ? | ? | Annual |

TABLE 1. Continued.

| Species | Family | Number of species Chile | Number of species total | Biogeographic element | Life form |
|---|---|---|---|---|---|
| *Leucheria* sp. | Compositae | 43 | 46 | ANDEAN | Annual |
| *Leucocoryne coquimbensis* F. Phil. | Liliaceae | 11 | 12 | ENDEM | Geophyte |
| *Leucocoryne purpurea* Gay | Liliaceae | 11 | 12 | ENDEM | Geophyte |
| *Leucocoryne violacescens* Phil. | Liliaceae | 11 | 12 | ENDEM | Geophyte |
| *Lithrea caustica* (Mol.) H. et A. | Anacardiaceae | 1 | 3 | TROP AM | Shrub |
| *Llagunoa glandulosa* (H. et A.) D. Don | Sapindaceae | 1 | 3 | ENDEM | Shrub |
| *Loasa tricolor* Ker-Gawl. | Loasaceae | 45 | 105 | ANDEAN | Annual |
| *Lobelia polyphylla* H. et A. | Campanulaceae | 8 | 365 | PANTROP | Shrub |
| *Malesherbia humilis* Poepp. | Malesherbiaceae | 18 | 27 | ENDEM | Annual |
| *Malva nicaensis* L. | Malvaceae | 3 | 30 | COSM* | Annual |
| *Malva parviflora* L. | Malvaceae | 3 | 30 | COSM* | Annual |
| *Marrubium vulgare* L. | Labiatae | 1 | 30 | COSM* | Perennial |
| *Medicago arabica* (L.) Hudson | Papilionaceae | 8 | 56 | COSM* | Annual |
| *Medicago polymorpha* L. | Papilionaceae | 8 | 56 | COSM* | Annual |
| *Melica* sp. | Gramineae | 14 | 70 | COSM | Perennial |
| *Melilotus indica* (L.) All. | Papilionaceae | 4 | 20 | COSM* | Annual |
| *Menonvillea* sp. | Cruciferae | 21 | 21? | ENDEM | Annual |
| *Mesembryanthemum cristallinum* L. | Aizoaceae | 1 | 70 | (2)* | Annual |
| *Moscharia pinnatifida* R. et P. | Compositae | 2 | 2 | ENDEM | Annual |
| *Muehlenbeckia hastulata* (J. E. Sm.) Johnst. | Polygonaceae | 1 | 15 | (3) | Shrub |
| *Mutisia* sp. | Compositae | 23 | 59 | ANDEAN | Perennial |
| *Myrcianthes coquimbensis* (Barn.) Landrum et Grifo | Myrtaceae | 1 | 1 | TROP AM | Shrub |
| *Nessella pubiflora* (Trin. et Rupr.) Desv. | Gramineae | 10 | ? | ANDEAN | Perennial |
| *Nolana crassulifolia* Poepp. | Nolanaceae | 13 | 18 | ENDEM | Shrub |
| *Nolana filifolia* (H. et A.) Johnst. | Nolanaceae | 13 | 18 | ENDEM | Shrub |
| *Nolana paradoxa* Lindl. | Nolanaceae | 13 | 18 | ENDEM | Annual |
| *Nolana sedifolia* Poepp. | Nolanaceae | 13 | 18 | ENDEM | Perennial |
| *Oenothera* sp. | Onagraceae | 17 | 80 | AMPHI | Annual |
| *Oenothera coquimbensis* Gay | Onagraceae | 17 | 80 | AMPHI | Annual |
| *Oenothera stricta* Ledeb. ex Link | Onagraceae | 17 | 80 | AMPHI* | Annual |
| *Ophryosporus triangularis* Meyen | Compositae | 4 | 38 | AMPHI | Shrub |
| *Oxalis gigantea* Barn. | Oxalidaceae | 115 | 500 | COSM | Shrub |
| *Oxalis maritima* Barn. | Oxalidaceae | 115 | 500 | COSM | Geophyte |
| *Oxalis micrantha* Bert. ex Savi | Oxalidaceae | 115 | 500 | COSM | Annual |

TABLE 1. Continued.

| Species | Family | Number of species Chile | Number of species total | Biogeographic element | Life form |
|---|---|---|---|---|---|
| *Oxalis rosea* Jacq. | Oxalidaceae | 115 | 500 | COSM* | Annual |
| *Oxybaphus elegans* Choicy | Nyctaginaceae | 4 | 45 | TROP AM | Perennial |
| *Paronychia chilensis* DC. | Caryophyllaceae | 5 | 50 | COSM | Perennial |
| *Pasithea coerulea* (R. et P.) D. Don | Liliaceae | 1 | 1 | ENDEM | Geophyte |
| *Pectocarya dimorpha* (Johnst.) Johnst. | Boraginaceae | 4 | 10 | AMPHI | Annual |
| *Pectocarya linearis* (R. et P.) DC. | Boraginaceae | 4 | 10 | AMPHI | Annual |
| *Phyla nodiflora* (L.) Greene | Verbenaceae | 3 | 15 | PANTROP* | Annual |
| *Plagiobothrys collinus* (Phil.) Johnst. | Boraginaceae | 17 | 100 | AMPHI | Annual |
| *Plantago hispidula* R. et P. | Plantaginaceae | 22 | 250 | COSM | Annual |
| *Plantago litorea* Phil. | Plantaginaceae | 22 | 250 | COSM | Annual |
| *Plantago* sp. | Plantaginaceae | 22 | 250 | COSM | Annual |
| *Pleocarphus revolutus* D. Don | Compositae | 1 | 1 | ENDEM | Shrub |
| *Plumbago coerulea* H. B. K. | Plumbaginaceae | 1 | 10 | PANTROP | Shrub |
| *Porlieria chilensis* Johnst. | Zygophyllaceae | 1 | 6 | ANDEAN | Shrub |
| *Proustia cuneifolia* D. Don | Compositae | 3 | 3 | ANDEAN | Shrub |
| *Puya berteroniana* Mez | Bromeliaceae | 7 | 168 | ANDEAN | Shrub |
| *Puya chilensis* Mol. | Bromeliaceae | 7 | 168 | ANDEAN | Shrub |
| *Puya venusta* Phil. | Bromeliaceae | 7 | 168 | ANDEAN | Shrub |
| *Quinchamalium chilense* Mol. | Santalaceae | 2 | 25 | ANDEAN | Annual |
| *Rhodophiala phycelloides* (Herb.) Hunz. | Amaryllidaceae | 28 | 76 | TROP AM | Geophyte |
| *Schinus polygamus* (Cav.) Cabr. | Anacardiaceae | 9 | 27 | TROP AM | Shrub |
| *Schismus arabicus* Nees | Gramineae | ? | 5 | COSM* | Annual |
| *Schizanthus litoralis* Phil. | Solanaceae | 13 | 13 | ENDEM | Annual |
| *Schizopetalon gayanum* Barn. | Cruciferae | 6 | 6 | ENDEM | Annual |
| *Senecio bahioides* H. et A. | Compositae | 222 | 1,500 | COSM | Shrub |
| *Senecio brunonianus* H. et A. | Compositae | 222 | 1,500 | COSM | Perennial |
| *Senecio cerberoanus* Remy | Compositae | 222 | 1,500 | COSM | Shrub |
| *Senecio hakeifolius* Bert. ex DC. | Compositae | 222 | 1,500 | COSM | Shrub |
| *Senna cumingii* (H. et A.) Irw. et Barneby | Caesalpiniaceae | 10 | 240 | COSM | Shrub |
| *Sicyos bryoniifolius* Moris | Cucurbitaceae | 1 | 25 | PANTROP | Annual |
| *Sisyrinchium cuspidatum* Poepp. | Iridaceae | 13 | 100 | TROP AM | Geophyte |
| *Sisyrinchium junceum* E. Mey. ex K. Presl. | Iridaceae | 13 | 100 | TROP AM | Geophyte |
| *Sisyrinchium scirpoideum* Poepp. | Iridaceae | 13 | 100 | TROP AM | Geophyte |
| *Solanum heterantherum* Witasek ex Reiche | Solanaceae | 64 | 1,400 | COSM | Annual |

TABLE 1. Continued.

| Species | Family | Number of species Chile | Number of species total | Biogeographic element | Life form |
|---|---|---|---|---|---|
| *Solanum nigrum* L. | Solanaceae | 64 | 1,400 | COSM* | Annual |
| *Solanum pinnatum* Cav. | Solanaceae | 64 | 1,400 | COSM | Shrub |
| *Sonchus asper* (L.) J. Hill | Compositae | 3 | 62 | COSM* | Annual |
| *Sphacele salviae* (Lindl.) Briq. | Labiatae | 3 | 25 | TROP AM | Shrub |
| *Sphaeralcea obtusiloba* (Hook.) D. Don | Malvaceae | 3 | 60 | AMPHI | Perennial |
| *Stachys litoralis* Phil. | Labiatae | 11 | 300 | COSM | Perennial |
| *Stachys truncata* Kunze ex Benth. | Labiatae | 11 | 300 | COSM | Perennial |
| *Stellaria cuspidata* Willd. | Caryophyllaceae | 8 | 120 | COSM* | Annual |
| *Stipa plumosa* Trin. | Gramineae | 44 | 150 | COSM | Perennial |
| *Tecophilaea violiflora* Bert. ex Colla | Tecophilaceae | 2 | 2 | ENDEM | Geophyte |
| *Tetragonia* sp. | Aizoaceae | 10 | 50–60 | COSM | Perennial |
| *Trichopetalum plumossum* (R. et P.) Macbr. | Liliaceae | 2 | 2 | ENDEM | Geophyte |
| *Triptilion* sp. | Compositae | 14 | 14 | ENDEM | Annual? |
| *Tristerix aphyllus* (Miers ex DC.) Van Tiegh. ex Barlow et Wiens. | Loranthaceae | 3 | 11 | ANDEAN | Hemiparasite |
| *Tropaeolum tricolor* Sweet | Tropaeolaceae | 18 | 86 | TROP AM | Perennial |
| *Tweedia confertiflora* (Decne.) Malme | Asclepiadaceae | 4 | ? | ANDEAN | Perennial |
| *Urtica urens* L. | Urticaceae | 11 | 45 | COSM* | Annual |
| *Valeriana bridgesii* H. et A. | Valerianaceae | 43 | 250 | COSM | Perennial |
| *Viola pusilla* Poepp. | Violaceae | 72 | 500 | COSM | Annual |
| *Vulpia* sp. | Gramineae | 5 | 20 | COSM | Annual |

(1) North and South America, Africa, and India.
(2) Mediterranean, California, South Africa, Canary Islands, Australia, Arabia, and Chile.
(3) South America, New Zealand, and Australia.

TABLE 2. Most important plant families in the flora of Lagunillas in the Chilean coastal desert and their relative representation in the flora of the high Andean desert (above 2,000 m) at 19°S in northern Chile, and in the flora of continental Chile.

| Family | Lagunillas | | High Andes* | | Flora of Chile** | |
|---|---|---|---|---|---|---|
| | NT | % | NT | % | NT | % |
| Compositae | 34 | 17.8 | 91 | 32.6 | 1,033 | 18.0 |
| Gramineae | 10 | 5.2 | 34 | 12.2 | 595 | 10.4 |
| Boraginaceae | 9 | 4.7 | 3 | 1.1 | 116 | 2.2 |
| Liliaceae | 8 | 4.2 | 0 | 0 | 50 | 0.9 |
| Papilionaceae | 7 | 3.7 | 12 | 4.3 | 321 | 5.6 |
| Onagraceae | 6 | 3.1 | 1 | 0.4 | 44 | 0.8 |
| Amaryllidaceae | 6 | 3.1 | 0 | 0 | 92 | 1.6 |

NT: Total number of species.
* Source: Arroyo et al. (1982).
** Source: Marticorena (1990).

LIFE-FORMS

Annual plants represent the highest proportion of the total flora (40.8%, Table 3), followed by shrub species (28.8%). Bulbous perennials represent 10.5% of the species. All the species that are seen aboveground only after the winter rains, i.e., annuals, geophytes, and rhizomatous perennial herbs, comprise 70.7% of the total flora.

NATIVE VERSUS INTRODUCED SPECIES

Fifteen percent of the species collected are introduced (Table 3), most of them annuals. If these exotic species are excluded from the analysis, annuals decrease their representation to 33.1% (Table 3). This results from the fact that one-third of the annual species are introduced. Thus, annual and shrub species represent equivalent proportions of the native flora of Lagunillas (Table 3). There were no exotic species among geophytes, and only one shrub species was introduced.

BIOGEOGRAPHIC ELEMENTS

Cosmopolitan genera represent a high proportion (41.4%) of the total flora (Table 4), being especially common among annual (55.1% of all annuals) and perennial herbs (54.1% of perennial herbs). Some of these species belong to weedy families; probably most have life-history traits that enable them to invade recently open habitats. In contrast, only 27.3% of the shrub species belong to Cosmopolitan genera. Species that belong to disjunct genera in North and South American deserts represent 15.2% of the flora (Table 4). This disjunct element includes 21.8% of the shrubs and 16.7% of the annual species. Endemic species amount to 13.1% of the total flora. Of these endemic taxa, 18 (72.0% of all endemics and 9.4% of the total flora) are restricted to the Chilean desert. The highest proportion of endemics is found among the geophytes and the lowest among the perennial herbs. Other important biogeographic elements in the flora of Lagunillas are the Andean and Tropical American (Table 4). The Andean element is more frequent among the annuals (11.6%) and shrub species (16.4%). Tropical-American elements are more represented among the geophytes (45%) than among species of any other life form.

TABLE 3. Percentage of total, native, and introduced species by life form in the flora of Lagunillas in the Pacific coastal desert of Chile. N = number of species.

| Life form | All species | | Native species | | Exotic species | |
|---|---|---|---|---|---|---|
| | N | %* | N | %* | N | %* |
| Annuals | 78 | 40.8 | 54 | 33.1 | 24 | 85.7 |
| Geophytes | 20 | 10.5 | 20 | 12.3 | — | — |
| Perennial herbs | 37 | 19.4 | 34 | 20.8 | 3 | 10.7 |
| Shrubs | 55 | 28.8 | 54 | 33.1 | 1 | 3.6 |
| Hemiparasite | 1 | 0.5 | 1 | 0.6 | — | — |
| Total | 191 | 100% | 163 | 85%** | 28 | 15%** |

* Percentages with respect to the totals below each column.
** Percentages with respect to the total number of species.

TABLE 4. Biogeographic elements by life form in the flora of Lagunillas. See text for definition of elements. N = number of species.

| Biogeographic element | Annuals | | Geophytes | | Perennial herbs | | Shrubs | | Total | |
|---|---|---|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | N | % | N | % |
| Cosmopolitan | 43 | 55.1 | 1 | 5.0 | 20 | 54.1 | 15 | 27.3 | 79 | 41.4 |
| Amphitropical | 13 | 16.7 | 1 | 5.0 | 3 | 8.1 | 12 | 21.8 | 29 | 15.2 |
| Endemic | 8 | 10.3 | 9 | 45.0 | 2 | 5.4 | 6 | 10.9 | 25 | 13.1 |
| Andean | 9 | 11.6 | — | — | 4 | 10.8 | 9 | 16.4 | 23 | 12.0 |
| Tropical American | — | — | 9 | 45.0 | 3 | 8.1 | 7 | 12.7 | 19 | 9.9 |
| Pantropical | 3 | 3.8 | — | — | 4 | 10.8 | 5 | 9.1 | 12 | 6.3 |
| Unclassified | 2 | 2.5 | — | — | 1 | 2.7 | 1 | 1.8 | 4 | 2.1 |
| Total | 78 | 100.0 | 20 | 100.0 | 37 | 100.0 | 55 | 100.0 | 191 | 100.0 |

## DISCUSSION

Most species in the flora of Lagunillas are annuals (Table 3), a large proportion of which (24 out of 78, or 30.8%) are non-native weeds. These weedy species are native to Eurasia, and their presence and abundance in the study area may reflect the recent history of farming and livestock raising in north-central Chile (Bahre, 1979). All of them are also found further south in the mediterranean region of Chile (Navas, 1979), particularly in abandoned pastures or agricultural land. It seems likely that many weed species that came with the Europeans colonized the coastal desert via central Chile.

Considering native species only, the percentage of annuals in the flora of Lagunillas in the Chilean coastal desert is higher than in high-altitude Chilean and North American deserts. Annuals represent between 10 and 29% of the flora above 2,000 m in the northern Chilean Andes (10–146 species), and 19% of the flora at 1,200 m in the Great Basin, U.S.A. (322 species), where plants are subjected to low temperatures in addition to the constraints in water availability (Arroyo et al., 1988). In contrast, the proportion of native annual species (33%) in the Pacific coastal desert site is lower than in other lowland deserts with less equitable temperature regimes. Annual species may represent 40–70% of the flora in Middle-Eastern deserts (Orshan, 1986), and 52–55% of the flora in the Sonoran and Colorado deserts of California (Richerson & Lum, 1980).

Although the number of species of geophytes is often lower than the species richness of other plant life forms, they represent a high proportion of the flora in the coastal desert. The relative importance of Liliaceae and Amaryllidaceae, the major bulbous taxa, in the flora of the coastal desert is higher than in high-altitude deserts in northern Chile (Arroyo et al., 1982) or in the flora of continental Chile (Table 2). Geophytes are also important components of the flora in the deserts of Israel, Afghanistan, and Iran (Breckle, 1983). In contrast, geophytes are less important in North American deserts (Shreve, 1942).

The representation of the various biogeographic elements in the flora of Lagunillas should provide insights into the history of the Pacific coastal desert vegetation. Based on the geological evidence about the origin of this desert (Ochsenius, 1982; Arroyo et al., 1988), it is reasonable to assume that the oldest elements of its flora originated from a tropical stock of woody taxa during the Eocene. Probable relicts from that period are arid-adapted Pantropical elements such as *Prosopis*, *Acacia*, *Caesalpinea*, and *Cordia* (Table 1), which are now widespread in dry subtropical environments (Sarmiento, 1972). The past and modern geographic ranges of these woody genera, which include arid to moist tropical and subtropical regions of America and Africa, suggest that they might have originated before the breakup of Gondwana was completed (Solbrig, 1976) in the early Tertiary. The low representation of Pantropical elements today (6.3%, Table 4) indicates, however, that many old tropical elements became extinct. It is likely that most of these Tertiary tropical elements disappeared due to the rapid and strong aridization that took place during the late Pleistocene–early Holocene (Ochsenius, 1982; Simpson, 1975). Consequently, most of the modern desert flora originated more recently, in direct relation to the uplifting of the Andes and the increasing aridity of the Pacific coast of South America during the Quaternary.

We propose that some of the modern desert genera (e.g., *Adesmia*, *Chaethantera*, *Loasa*, *Mutisia*, *Porlieria*, and *Puya*) diversified in the Andean highlands and invaded the lowland desert subsequently. All of these South American genera have a large number of species (Table 1), which are mostly restricted to the Andes.

Pacific coastal desert endemics represent the third most important element in the flora (Table 4). Two subgroups can be recognized among the desert endemics. Some endemic genera appear to have diversified very recently in the coastal desert area (Mesa, 1981), exhibiting a high number of species per genus (e.g., *Cristaria*, *Malesherbia*, *Nolana*, Table 1), probably extending their ranges into the Andean environment (F. Squeo, unpublished manuscript on the genus *Malesherbia*). On the other hand, other low-diversity genera, which are often monospecific and have a geographic distribution restricted to one or a few localities in the Pacific coastal desert (e.g., *Ancrumia*, *Bridgesia*, *Llagunoa*, *Pasithaea*, *Phleocarpus*, *Reichea*) may represent remnants of a pre-aridization subtropical flora. In the latter group we could also include some Tropical American genera (e.g., *Alonsoa*, *Cestrum*, *Colliguaja*, *Oxybaphus*, *Sphacele*) that have a lower specific diversity in Chile (Table 1) than in the rest of South America.

A considerable proportion of the taxa belong to an element with a disjunct distribution in the deserts of South and North America. Because these species are presently restricted to arid lands, it is hard to explain how they may have reached their present distribution without assuming that arid habitats extended through the lowland tropics during the last glacial period or earlier (e.g., Simpson & Neff, 1985). Raven (1963) argued that most of these disjunct species could have migrated from South to North America across the Tropics, taking advantage of hypothetical subhumid sites in post-Miocene times. This hypothesis assumes that these species are capable of long-distance dispersal (Raven, 1963); however, this dispersal ability is seldom found among xerophytic species (Ellner & Schmida, 1981). For a majority of the disjunct taxa in Lagunillas (e.g., *Cardionema*, *Camassia*, *Encelia*, Table 1), it is hard to argue in favor of the long-distance dispersal hypothesis. The present distribution of these disjunct elements provides support for the hypothesis that arid environments extended through the area of the lowland Tropics during the last glacial period (Simpson & Neff, 1985). For some of the annual species (e.g., *Clarkia*, *Gilia*, *Camissonia*), dispersal associated with humans in modern times seems a more likely explanation.

An important component of the flora of the study site is the Cosmopolitan element. A major proportion of these Cosmopolitan taxa are annual and perennial herbs (Table 4). Because of their widespread distribution, it is likely that many of them could have been introduced by humans in recent times (e.g., *Erodium*, *Galium*, *Schismus*).

Because deserts are relatively open environments of recent origin (Arroyo et al., 1988), we expect that short-lived, opportunistic species, with high reproductive capacity, may contribute an important proportion of their flora.

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# EVOLUTION OF REPRODUCTION IN *LAMPROTHYRSUS* (ARUNDINEAE: GRAMINEAE)

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ABSTRACT

*Lamprothyrsus*, a ditypic arundinoid, South American grass genus, consists predominantly of populations of exclusively female plants in which seeds are set by autonomous apospory. *Lamprothyrsus peruvianus* is a high polyploid—$2n$ = ca. 136, the highest chromosome number so far recorded in the Arundineae. The hypothesis favored here for the evolution of apospory involves a mutation for apomixis spreading through to fixation in an old, dioecious, polyploid genus resulting in generations solely of female plants. This proposal is consistent with reproductive pathways already recognized in some aposporous species of the related genus *Cortaderia*, and in some diplosporous species of *Poa* and *Calamagrostis*. It is another example of the association between apomixis and dioecism outlined by Gustafsson 45 years ago.

*Lamprothyrsus* is an arundinoid genus erected by Pilger (1906) to accommodate South American grasses with long, erect, hyaline, lateral lemma lobes and even longer, stiffer, recurved to reflexed awns; two species are now recognized: *L. peruvianus* Hitchc., primarily from Ecuador and Peru, and *L. hieronymi* (O. Kuntze) Pilger from Bolivia and northern Argentina. The genus is unique within the Gramineae in that it is the only one where almost all plants are female, and reproduction is solely from seeds set autonomously apomictically (Connor, 1979; Parodi, 1949). Because its affinity lies clearly with austral *Cortaderia* (Conert, 1961, 1987; Clayton & Renvoize, 1986), *Lamprothyrsus* might be suggested as an end of one evolutionary line of the cortaderioid facies of the tribe Arundineae. Its chromosome numbers are, therefore, of particular interest. Here we report a highly polyploid somatic number for *L. peruvianus*, and discuss its significance in the Arundineae and in the evolution of the reproductive biology of the genus.

## CHROMOSOME NUMBER AND REPRODUCTION

### THE PLANTS

One of us (H. Connor) collected seeds of tall and tussock-forming *L. peruvianus* between Tarma and San Ramon, Departmento Junín, at 2,300 m in the Peruvian Andes in August 1975; 100 plants were grown in the gardens of Botany Division, DSIR, Lincoln, New Zealand. All plants were monomorphic females—male-sterile—and of the floral form illustrated for *Lamprothyrsus* by Bernadello (1979) and Nicora & Rúgolo de Agrasar (1987), and have remained unchanged for 17 years in cultivation. All plants set seed abundantly by autonomous apospory where the embryo sac develops from the nucellus (Connor, 1979, 1987; terminology after Nogler, 1984). These seeds germinate freely.

### CHROMOSOME NUMBER

The count obtained for *L. peruvianus* is $2n$ = ca. 136 (Fig. 1); voucher CHR 449637. The chromosomes are small (0.7–2.4 μm). This is the highest reported number for the Arundineae, though it is very close to $2n$ = ca. 132 reported for *Phragmites australis*. High levels of polyploidy are already recognized in the tribe; among the highest numbers are:

1. $2n$ = ca. 132 = $11x_2$ : *Phragmites australis* (Cav.) Steudel, cited as *P. communis* Trin. in papers prior to Clayton (1968); Gorenflot, 1986)
2. $2n = 120 = 10x_2$ : *Rytidosperma indutum* (Vickery) Connor & Edgar (Brock & Brown, 1961, as *Danthonia*)
3. $2n = 108 = (18x)$ : *Arundo donax* L. (Christopher & Abraham, 1971)
   $= 12x$ : *Cortaderia jubata* (Lem.) Stapf (Connor & Edgar, 1974)

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FIGURE 1. Metaphase of mitosis in *L. peruvianus*, × 3,000; $2n$ = ca. 136.

: *C. rudiuscula* Stapf, in plants raised from seeds collected (by H. Connor) at the *locus classicus*, Santa Rosa de Los Andes, Chile; voucher CHR 468718. This is the first report for this taxon.

4. $2n = 96 = 8x_2$ : *Rytidosperma* spp. (Brock & Brown, 1961)
: *Phragmites australis* (Lenoir et al., 1975; Gorenflot et al., 1984)

5. $2n = 90 = 10x$ : *Cortaderia* spp. (Hair & Beuzenberg, 1966)

6. $2n = 72 = 6x_2$ : *Rytidosperma* spp. (Brock & Brown, 1961)
: *Monachather paradoxus* Steudel (Brock & Brown, 1961, as *Danthonia bipartita*)
: *Phragmites australis* (Gorenflot et al., 1984; Lenoir et al., 1975; Pohl & Davidse, 1971)
$(12x)$ : *Arundo donax* (Christopher & Abraham, 1971)
$(12x)$ : *A. plinii* Turra (Fernandes & Queirós, 1969)
$= 8x$ : *Cortaderia* spp. (Connor & Edgar, 1974)

The basic number for *Arundo* species is uncertain; the levels of ploidy shown in parentheses are based on the assumption that $x = 6$.

The chromosome number sometimes varies among populations. Of the taxa listed above, those with variable chromosome numbers are:

*Arundo donax* $2n$ = ca. 60, 72, 108, 110 (Christopher & Abraham, 1971; Fernandes & Queirós, 1969; Larsen, 1963)
*Phragmites australis* $2n$ = 36, 42, 44, 46, 48, 49, 50, 51, 52, 54, 72, 84, 96, 132 (Gorenflot et al., 1984; Gorenflot, 1986)
*Rytidosperma indutum* $2n$ = 72, 96, 120 (Brock & Brown, 1961)
*R. caespitosum* (Gaudich.) Connor & Edgar $2n$ = 24, 48, 72 (Brock & Brown, 1961)
*R. laeve* (Vickery) Connor & Edgar $2n$ = 24, 48, 72 (Brock & Brown, 1961)
*R. linkii* (Kunth) Connor & Edgar $2n$ = 24, 48, 72 (Brock & Brown, 1961)

Even allowing that the chromosome count for *L. peruvianus* is approximate, it does not fit any of the usual arundinoid range of basic numbers indicated above, viz $x = 6$, $x = 9$, $x_2 = 12$, nor does it fit with a cytologically isolated genus such as New World *Gynerium*, $x = 11$ (Pohl & Davidse, 1971), nor with austral, Old World *Chionochloa*, $x = 7$ (Dawson, 1989).

REPRODUCTION IN HIGH POLYPLOID ARUNDINOIDS

Reproduction is sexual in high polyploid arundinoids; the exception is gametophytic apomixis in female plants in the two species of *Lamprothyrsus*, and in at least six species of *Cortaderia* (Bernadello, 1979; Connor, 1965, 1973, 1979, 1983a, b, 1987; Costas-Lippmann, 1979; Parodi, 1949; Pohl & Davidse, 1971; Philipson, 1978). Gender diversification is an uncommon evolutionary step in the tribe as a whole and, *Lamprothyrsus* and *Cortaderia* apart, is seen only in dioecism in monotypic *Gynerium*, in gynodioecism in one species of *Chionochloa*, and in andromonoecism in *Alloeochaete* and *Phragmites* (Connor, 1990).

Asexuality in females evolved in *Lamprothyrsus* and *Cortaderia* in the identical form of autonomous (nonpseudogamous) apospory after dioecism, subdioecism, or gynodioecism had become fixed as gender dimorphisms (Connor, 1987). Further, megagametogenesis is similar in both; the embryo sac, nucellar in origin, is commonly 6-nucleate, since one synergid and one antipodal are absent (Philipson, 1977, 1978; M. N. Philipson in Connor, 1987). Philipson & Connor (1984) examined the megagametophyte of eight genera of the Arundineae for haustorial synergids; they were present in *Lamprothyrsus*, *Cortaderia*, *Danthonia*, *Sieglingia*, *Rytidosperma*, and *Pyrrhanthera*, but absent from *Arundo* and *Phragmites*. There is no correlation between apomixis and haustorial synergids, because sexual reproduction is recorded in all genera except *Lamprothyrsus*.

Sexual reproduction in andromonoecious *Phragmites australis* is not very successful, as estimated from seed setting (Cartier & Lenoir, 1980; Gustafsson & Simak, 1963; Luther, 1950), even though megagametogenesis is normal (Cartier & Lenoir, 1980) and pollen fertility is high (Lenoir et al., 1975; Stoian et al., 1974). Large colonies of single, self-incompatible genotypes may be one cause, but the instability of chromosome number reported by Gorenflot et al. (1984) and Lenoir et al. (1975) could contribute in small part. Richards (1986) suggested that in northern English and Scottish populations ". . . summer temperatures are too low for seeds to ripen adequately." There is no suggestion of apomixis in *Phragmites*.

*Arundo donax* is less variable in chromosome complement than *P. australis*. All flowers are perfect. The only information we have on reproductive biology indicates that many megagametophytes fail to mature (Gustafsson, 1947; Philipson & Connor, 1984).

Sexual reproduction is usually cleistogamous in *Monachather*, and either chasmogamous or cleistogamous in *Rytidosperma* (Brock & Brown, 1961; Cashmore, 1932). *Monachather* is an extremely specialized monotypic genus of eremaean Australia; *Rytidosperma* is especially well developed in Australasia (Connor & Edgar, 1986).

*LAMPROTHYRSUS*

MALE-FERTILITY

Although there are substantial reports that *Lamprothyrsus* sets seeds exclusively on female plants in the absence of pollen, Bernadello (1979) recorded two specimens of *L. hieronymi* with polliniferous anthers: one from northern Argentina (*Fabris 3491*, 1962), and the other from Bolivia (*Steinbach 3453*, 1917). Foster (1966) had cited *Steinbach 3453* in GH without reference to its sex-form; it is male (E. A. Kellogg, in litt.). In the flowers of both, as illustrated by Bernadello (1979) and by Nicora & Rúgolo de Agrasar (1987), the anthers are large and the gynoecia small; the flowers cannot be interpreted as female flowers with male-fertile anthers. Both sex-forms are directly comparable with the dimorphic floral syndrome in *Cortaderia* (Connor, 1973).

Pollen in the male flowers of *L. hieronymi* is viable (Bernadello, 1979); we assume that it could lead to fertilization in normally reduced embryo sacs. This would necessitate strict sexuality in some plants, or the co-occurrence of sexual embryo sacs with aposporous sacs—this latter is frequent enough in gametophytic apomictic grasses. However, for the greater part plants will have produced unreduced aposporous embryo sacs; to add to the difficulty, at the time of anthesis precocious embryogenesis and endosperm formation is already well advanced. Female plants of that type would need to re-regulate the maturation of the gynoecium to allow the sequence of pollination at anthesis, pollen tube growth, and fertilization. Gynoecia in polliniferous plants are imperfectly developed as Bernadello (1979) reported, and as the Argentinian and Bolivian specimens of *L. hieronymi* show; it seems very unlikely that fertilization and seed set would occur there. Any of the benefits deriving from a generation of sexual reproduction that male plants could interpose into persistent asexuality (Lynch & Gabriel, 1983) would seem denied to *Lamprothyrsus* because the chances of males contributing genes to the next generation are very slight.

The presence of two polliniferous plants in *L. hieronymi* suggests, of course, that there may be more male plants in the populations than the herbarium collections reveal, but this needs to be es-

tablished. Should there be other male plants, explicit dioecism may be current, and asexual reproduction, though predominant, may not be exclusive. Synchronous maturation and anthesis of male and female elements would lead to sexually reproduced seeds. Nevertheless, genes for asexuality would be successfully invading the populations to the detriment of dioecism, so these two male plants could be among the last of the male remnants of that species. The count of one male plant in about 100 specimens listed by Bernadello (1979) for the whole of its Argentinian range may support this proposition.

The two male plants may only represent a low frequency sporadic mutation for the restoration of male-fertility, which brought with it the correlative changes in the gynoecium characteristic of dioecism and gynodioecism in the Arundineae. Such a mutation would be simpler if male-sterility was genetically controlled as in *Cortaderia* (Connor & Charlesworth, 1989) than if the nuclear-cytoplasmic system common to wild plants (Couvet et al., 1986) was operating.

It seems improbable that the male plants are the residue of a pseudogamous system because, as Asker (1980) has pointed out, pseudogamy is an unlikely precursor to non-pseudogamy; further, the two states never co-occur in one agamic complex. The synchrony essential to sexual reproduction would also be prerequisite of pseudogamy.

To date, polliniferous plants are unreported in *L. peruvianus*, but they are as possible in this species as in *L. hieronymi*. They would be accompanied by the same benefits, limitations, or constraints already outlined for *L. hieronymi*.

## EVOLUTION OF APOMIXIS

Pathways to the formation of populations consisting exclusively of female plants usually involve hybridism at some level; another associate is dioecism (see Westergaard, 1958). There is also a close correlation between hybridism, high levels of polyploidy, and apomixis.

*Lamprothyrsus*, with two oreophilous species, would be best interpreted as the contemporary, asexual residue of an old, austral, allopolyploid genus that had become dioecious, but which later substituted autonomous apospory in females for the sexual functions of dioecism. A mutation for apomixis spreading through females in 1M : 1F dioecious populations can readily lead to fixation (Charlesworth, 1980; Crowe, 1988; Lloyd, 1980; Marshall & Brown, 1981; Maynard Smith, 1971). Clearly, this pathway has been followed in apomictic South American species of *Cortaderia* (Connor, 1973, 1983b). Some diplosporous species of *Poa* and *Calamogrostis* have similar histories (Kellogg, 1990).

That hypothesis avoided any direct role for hybridism in the evolution of apomixis, although the high level of polyploidy indicates an amphiploid origin for taxa in *Lamprothyrsus*. Amphidiploidy itself neither assists nor hinders the development of an agamospermous system, but amphiploids will more easily accommodate occasional restoration of male-fertility.

What selection pressures would have favored the adoption of an autonomous apomixis in a dioecious taxon? It would be idle to invoke attractive ideas such as climatic conditions becoming unfavorable to the maturation and dispersal of pollen so that males became of lowered fitness; or that the sex-forms became overdispersed and exceeded pollination distances; or that sexual reproduction became limited by the ecological separation of the sex-forms as recorded by Fox & Harrison (1981) for *Festuca*, and by Freeman et al. (1976) for *Distichlis*, but undetected in *Buchloe dactyloides* (Quinn, 1991; Shaw et al., 1987) or in any of four Australian dioecious grass genera (Connor & Jacobs, 1991). Speculation about those forces should remain speculation; nevertheless, any increase in pollen fitness that was expected with the evolution of dioecism has been foregone, and with it male heterogamety. But all plants produce seeds, not half of them; and precocious embryogenesis allows the benefit of the development of seeds before both panicle emergence and anthesis.

It is evident that the maternal fitness and heterozygosity incorporated by autonomous apomixis remains high if measured in *Lamprothyrsus* by contemporary ecological versatility, and by morphological variability (Bernadello, 1979; Conert, 1961; Pilger, 1906), even though apomixis is generally not thought to be selected to increase ecological or evolutionary potentialities. Gabriel (1988) showed that apomicts, through both mutation and selection, could maintain a high level of genetic variability, and that they could be expected to perform well even in ecologically unstable environments. However, as Kellogg (1990) correctly observed, little is known of the patterns of variability in *Lamprothyrsus*, and both Conert's (1961) and Pilger's (1906) taxonomic attempts at accounting for infraspecific variation in *L. hieronymi* were unacceptable to Bernadello (1979).

*Lamprothyrsus* as a genus is predominantly autonomously apomictic in reproduction; such a state in the Gramineae is approached only by monotypic

*Nardus*, where apomixis may be autonomous; but there it is diplosporous, not aposporous, and is not exclusive (Rychlewski, 1961). All flowers are perfect and protogynous. Nogler (1984) felt that *N. stricta* L. should be reinvestigated because some critical data are unavailable.

Dioecious grasses are significantly a New World phenomenon; the greatest number of dioecious genera is in Mexico (Reeder, 1969). In none of them is there any known departure from sexual reproduction save for *Lamprothyrsus* and *Cortaderia*. It seems unlikely that there is a common ecological element, other than mountain environments, associated with the evolution of a specialized form of gametophytic apomixis, which supplanted a system already specialized in gender diversification. The explanation for the selection of this pathway must lie in reproductive efficiency, or in fitness. *Lamprothyrsus* offers an opportunity for evolutionary study as unique as itself. It is yet another example of the association between dioecism and apomixis elaborated by Gustafsson (1947).

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# FIRST REPORT OF BALLISTOCHORY IN THE POACEAE[1]

*Tatiana Sendulsky*[2]

ABSTRACT

A newly described mode of fruit dispersal mechanism in bambusoid grasses of the genera *Sucrea* and *Raddia* (Poaceae: Bambusoideae: Olyreae), previously unknown, is here discussed.

Fruit dispersal in grasses (Poaceae) occurs in many different ways. The dispersal units (diaspores) mostly consist of caryopses protected by their bracts, which may be equipped with a variety of straight or twisted awns, bristles, hooks, pointed calluses, harpoonlike hairs, feathery plumes, and special tissues for buoyancy. Alternatively, they may have none of these specialized structures. In this case the dispersal unit may be composed of the whole spikelet, the caryopsis with its lemma and palea, or the naked caryopsis alone, with no protecting bracts; all three types fall as they are to the ground. There are other modes of dispersal: wind, rainwash for short distances, streams, rivers, and even the sea, termites, ants, birds, fish, and through a variety of means of transportation, intentional or unintentional, related to humans (van der Pijl, 1982; Sendulsky, 1965, 1966; Davidse, 1987; Filgueiras, 1986; Silberbauer-Gottsberger, 1984; Sendulsky et al., 1987).

These modes of dispersal in grassland grasses usually depend on one principal condition—the dry state of the mature dispersal unit. Thus caryopses, enclosed in their dry bracts with dry hairs and plumes, are light and easily carried by the wind. The awns, sharp-pointed calluses, and hooks become harder when dry and adhere better to fur or clothing. Only dry bracts let the anthecium or the caryopsis loose so that it falls easily to the ground.

A completely different condition for dispersal of diaspores is required by some genera of herbaceous bambusoid grasses. These grasses belong to the large subfamily Bambusoideae and "are not grassland grasses but are confined to warm and humid environments, within forests, usually under dense shade" (Soderstrom & Calderón, 1974).

According to Soderstrom & Calderón (1980), in 1972 and 1976 they collected about 162 different species of Bambusoideae in Brazil; of these, 80 were undescribed or new to science. At the time about 12 species of *Raddia* and a few species of *Sucrea* and of *Eremitis*, most of them still undescribed, were brought under cultivation in the Rio de Janeiro Botanical Garden by Dimitri Sucre, who accompanied Soderstrom in fieldwork in Espírito Santo and Rio de Janeiro.

In 1972, living samples of each species of these bambusoid grasses were given to me by Sucre and I started a living collection, which I still have in my office at the Instituto de Botânica in São Paulo, Brazil. Among known species there are *Raddia brasiliensis* Bertol., *R. distichophylla* (Schrad.) Chase, and the recently described *Sucrea maculata* Soderstrom. These species have revealed an unusual fruit dispersal mechanism that I could never have discovered by simply collecting, preparing, and studying the dried plant specimens.

At first I was surprised by the appearance of seedlings of different species of *Raddia* and *Sucrea maculata* in pots occupied by other plants, at a distance of 1.5–2 m from the mother plants that had produced the fruits. The mystery was explained one hot evening when I was working late in the office. Preceded by a quiet "click," a fruit flew

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and fell on my desk. I went to the plant, the branches of which were in slight movement, to see how it had happened; my first attempts to catch a fruit failed; the fruits were much faster than I was. Finally I caught one within its spikelet and had to hold it firmly, feeling the strong movement of the bracts between my fingers as I carried it to the microscope.

## Dispersal

Herbaceous bamboos live mainly in humid tropical forests, where there is little or no wind; anemochory, one of the common modes of dispersal in grasses, is substituted in the bambusoid grasses mentioned above by autochory, i.e., the dispersal of the diaspores by the plant itself, using ballistic movement, which depends upon the turgor or volume pressure in its cells and on the different anatomical structures of the two sides of the glume. The diaspore of the *Raddia* species and of *Sucrea maculata* is composed of the caryopsis with its lemma and palea, which wrap tightly around it and form the anthecium. At the base of the anthecium there are two green glumes, firm in texture, as long as a spikelet or longer; these glumes are responsible for the rapid ejection of the anthecium.

The irritability of the plant, and the response that produces the movement, depend on factors that may act as a stimulus. According to *Strasburger's Textbook of Botany* (Harder et al., 1967: 393), "This stimulus releases a complicated series of reactions in the living material, the energy for which comes from the organism itself and not from the initial stimulus." Thus, during an investigation of the catapult phenomenon in herbaceous bambusoid grasses, two kinds of factors were distinguished that may act as stimuli.

### External factors

*High temperature.* On hot summer days, the plant increases its ballistic activity (pers. obs.).

*Wind, drops of water, contact with insects or animals, or any mechanical touch.* The ripe diaspores are very sensitive to the slightest touch; a drop of water, an insect, or a slight breeze may trigger ballistic movement.

### Autonomous factors that are within or arise within the plant itself

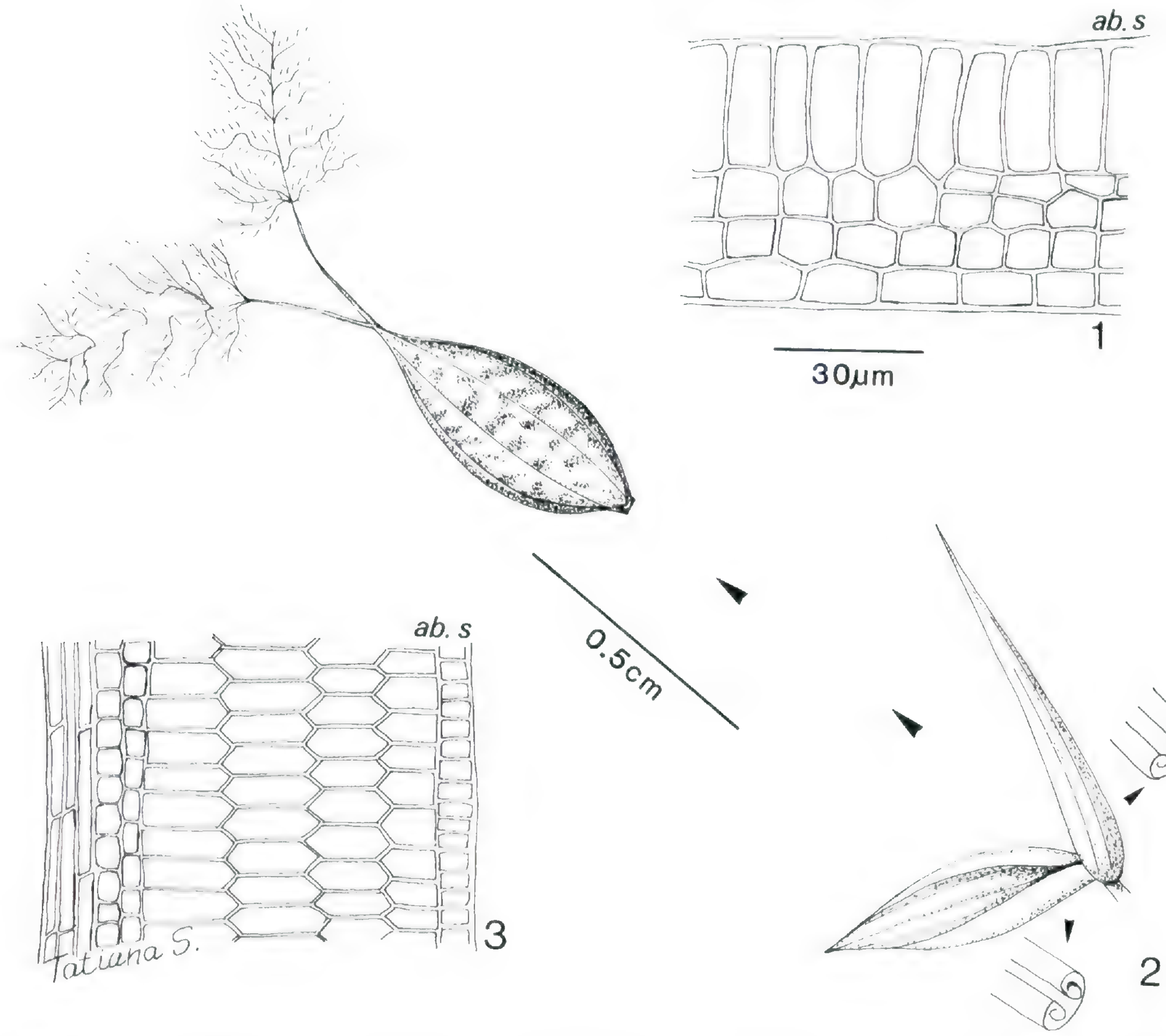
*Accelerated ripening of the fruit.* The anthecium, when being ejected, is fully formed but still bears white, fresh, plumose stigmas, which indicate the rapid development of the caryopsis from the moment of pollination to the phenomenon of ejection. The plant has to produce ripe diaspores before the glumes become dry and withered, as this will prevent them from producing the catapult process, which depends on the turgor pressure in the cells. At the moment of dispersal, the diaspore and glumes must be full of water and turgid. Here lies the main difference in conditions for dispersal in grassland grasses and in this group of herbaceous bambusoid grasses.

*Weight and surface of the anthecium.* The mature anthecium, in order to be effective, has to be heavy, while its surface is very smooth. These combined factors permit more speed, as the anthecium slips from the glumes, and increase its trajectory.

*Nyctinastic movement.* The sleep movements of the leaves, which were observed in *Sucrea maculata* and in all species of *Raddia*, often cause ejection of the diaspores. When the dense, fernlike leaves start their upward and downward movement, they sometimes get caught against each other; continuous movement causes the leaves to jerk free and the plant, or a few of its branches, swings. This sudden jerk or swaying of the branches is enough to elicit dispersal.

*Difference in anatomical structure.* The dorsiventrality of the glumes of bambusoid grasses involves inequality of the cells on the two sides of the glumes; this is necessary for nastic movement. The external (abaxial) side of the glume consists of large, uniform, narrow, uprightly arranged, thin-walled epidermal cells, twice as large as those of the internal (adaxial) side (Fig. 1). The cells of the external side tend to expand transversally because of their form, density, tightness, and turgor. The internal side consists of smaller flat cells. When the turgor in the cells of the external side reaches its maximum, the layer of the cells of the internal side resists the expansion of the external layer. But there comes a moment when, as the result of some metabolic process, or the response to a certain stimulus, the internal side cells suddenly lose tension and cease to resist. The volume of the internal side suddenly decreases, while that of the external side increases.

*Abscission of the anthecium.* The turgid ripe anthecium, clasped tightly by its turgid glumes, holds the state of tension. The moment of abscission is important; the anthecium separates from the pedicel at its base and above the insertion of the glumes. This is decisive for ejection, equal to the phenomenon of the abscission of the middle lamellae




FIGURES 1–3. Ballistic movement. — 1. Transversal section of a glume of *Sucrea maculata*. — 2. Flying diaspore of *Sucrea maculata* (glumes in lower right, anthecium in upper left). — 3. Longitudinal section of the fruit wall of the *Impatiens* species. Schematical representation, based on Strasburger (Harder et al., 1967). Abbreviation: ab. s. = abaxial side.

mellae in *Impatiens* spp., Balsaminaceae (Harder et al., 1967). As a result, the anthecium starts its slipping movement out of the tight glumes, and simultaneously the sides of the glume start from the base to roll in upon themselves forming four springs, which fling the anthecium 1.5–2 m (Fig. 2).

Ballistichory in *Impatiens* basically depends on the interaction between the thin-walled parenchyma cells of the external layer (expansion tissue) and the smaller collenchyma cells of the internal layer (resistance tissue) of the fruit wall (Harder et al., 1967; Fahn, 1974).

Comparison of the longitudinal sections of the fruit of *Impatiens* species with the cross section of the glume of *Sucrea maculata* makes clear the similarity in anatomical structures of the fruit wall and the glume. A rather fleshy fruit of *Impatiens* species (Fig. 3) presents four layers of thin-walled parenchyma cells on the external side and two or three layers of collenchyma cells on the internal side; the glume, a thin organ in *Sucrea maculata*, has only one layer of large, thin-walled epidermal cells on the external side, one layer of smaller cells on the internal side, and two layers in between, consisting of the mesophyll cells with chloroplasts.

In spite of the fact that the contraction of these dissimilar organs (fruit wall of *Impatiens*, glumes of grass) proceeds in different directions (longitudinally in the fruit wall and transversely in the glume), the catapult mechanism is the same in these plants, which thus tend to escape the shade of the mother plant.

The dispersal of diaspores by means of ballistic movements in the Poaceae was previously unknown; it is hoped that these observations on this

mode of dispersal in the herbaceous bambusoid grasses will serve as a guide for further research.

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**Cover illustration.** *Pleurothyrium giganthum* van der Werff, by J. Myers.

# Annals of the Missouri Botanical Garden 1993

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# *rbc*L SEQUENCE DATA AND PHYLOGENETIC RECONSTRUCTION IN SEED PLANTS: FOREWORD

*Gerard Zurawski*[1] *and Michael T. Clegg*[2]

When asked to write a brief foreword to this volume, we wondered what, if anything, needed to be said. Certainly the articles presented here speak for themselves about the current and future impact of comparative *rbc*L sequencing on plant phylogenetics. In the end, we felt it might be useful to describe briefly our view of the history that has led to this large and highly cooperative effort in systematics. For us at least, the history is important because it illustrates the interlocking nature of biological research.

The key players in this story include geneticists, biochemists, molecular biologists, biometricians, systematists, private industry, and national funding agencies. This diverse group laid the framework for what must surely be regarded as the most exciting effort in plant systematics in recent decades. Where did it all begin? One starting point was the discovery that some cytoplasmic organelles have their own DNA molecule. Another starting point was the suggestion by Zuckerkandl and Pauling in 1965 that the topology of branching of evolutionary trees could be inferred from the accumulation of amino acid substitutions in proteins.

The phenomenon of cytoplasmic inheritance provided the first tantalizing hints that extranuclear DNA molecules might exist in plant and animal cells. Wildman showed that an abundant protein fraction in plant cells called the "Fraction 1 Protein" was transmitted cytoplasmically in tobacco. Later, in the mid-1960s, it was established that the chloroplast and mitochondrial organelles contained DNA molecules. The Fraction 1 Protein was shown to be a component of the enzyme ribulose-1,5-bisphosphate carboxylase, responsible for fixing $CO_2$ in photosynthesis. Most work during the early 1970s was directed toward establishing the physical characteristics and size of the chloroplast DNA (i.e., that it is a closed circular molecule with an average GC content of about 38%). Beginning in the mid to late 1970s the new tools of recombinant DNA technology were aggressively applied to the study of the chloroplast genome. Because the chloroplast genome is relatively small and because chloroplast DNA constitutes an abundant fraction of total cellular DNA, most workers in the embryonic field of plant molecular biology focused on the study of the chloroplast genome. A problem

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of nearly universal interest was the cloning and sequencing of the large subunit of ribulose-1,5-bisphosphate carboxylase (*rbc*L, the gene for Fraction 1 Protein). McIntosh, Poulsen, and Bogorad were the first to achieve this feat in 1980 by defining the *rbc*L sequence from maize.

Our involvement in this story began in 1981. One of us (M. Clegg) was a Sabbatical Visitor in the laboratory of Whitfeld and Bottomley at the Division of Plant Industry, C.S.I.R.O. in Canberra, Australia. The proposed research was to utilize RFLP analysis of chloroplast DNA to define relatedness between various modern and ancient barley cultivars. G. Zurawski was a Research Fellow in the same laboratory and had recently completed the *rbc*L sequence from spinach and was starting the pea *rbc*L sequence. A casual comment by G.Z. to M.C. expressed an opinion that "RFLP analysis is fine, but why wouldn't you want to comparatively sequence part of the barley chloroplast genomes—you would be dealing with many more base changes and they would be fully defined." This conversation prompted a determination by M.C. to learn DNA cloning and sequencing and was the beginning of our enduring collaborative friendship.

The next part of our story continued in the laboratory of G.Z. at the DNAX Research Institute of Cellular and Molecular Biology in Palo Alto, California. We spent a couple of hectic weeks together (M.C. as a Sabbatical Visitor) completing the sequence of *rbc*L and *atpβ* genes from three diverse lineages of barley. Comparisons of the maize and spinach *rbc*L sequences indicated a high degree of similarity between taxa that represented the two classes of flowering plants. However, the extent of this similarity did not prepare us for the complete absence of nucleotide differences between our hard-earned barley sequences. This result appeared remarkable in view of the moderate to high levels of nuclear gene polymorphism common in barley and most other plant taxa. Comparison of the maize and barley *rbc*L sequences established that the rate of substitution was on the order of $1 \times 10^{-9}$ substitutions per synonymous site per year, a very low value. Surprisingly, our friendship survived the hard work required to establish this low value. Soon after, comparisons of cyanobacterial and flowering plant *rbc*L sequences (with S. E. Curtis) confirmed the slow rate of evolution of this chloroplast-encoded gene over the whole sweep of plant evolution. It was clear from these initial results that the DNA sequences from slowly evolving chloroplast genes could be used to reconstruct plant phylogeny at its deepest levels.

A detailed statistical analysis of the limited number of *rbc*L sequences available in 1985 (with K. Ritland) showed that *rbc*L gene sequences could indeed be used for the reconstruction of plant evolutionary history. Despite these encouraging results, it was still a difficult and laborious task to sequence a gene from any given plant taxon. The Maxam-Gilbert method of chemical modification was the standard sequencing approach of the early 1980s. This method required detailed restriction mapping and the construction of elaborate sequencing strategies for its implementation. The time from initial preparation of DNA through to cloning a chloroplast gene and to determining its sequence frequently required six months of labor.

In parallel with work on chloroplast gene sequences, Palmer and collaborators were establishing the utility of chloroplast DNA restriction site analyses for the study of plant relationships. This work captured the attention and imagination of the systematics community and attracted a large number of imaginative, young systematists to the use of molecular data for phylogenetic analysis.

Three developments laid the foundations for the mass of coordinated data presented in this issue of the *Annals*. The first was the adoption of a sequencing protocol that utilized Sanger dideoxy-sequencing together with a standard set of *rbc*L primers. The *rbc*L primers were based on sequences that were conserved between the two distantly related taxa (maize and spinach). Preliminary work with D. E. Giannasi showed that this primer set worked well for sequencing other plant *rbc*L genes. The set of primers was made freely available to the scientific community courtesy of DNAX Research Institute of Molecular and Cellular Biology (supported by Schering-Plough Corporation). The second major development was the invention of the polymerase chain reaction method (PCR). The PCR method eliminated the cumbersome and time-consuming operations of molecular cloning. These two developments have led to a rich and exciting database that is the subject of this issue. The third parallel development was the explosive growth in computing power experienced in the 1980s and the widespread dissemination of algorithms for phylogenetic inference by Swofford and by Felsenstein. This issue is the culmination of these three developments, and in a larger sense it is the culmination of independent research trends in disciplines ranging from the chemistry of nucleic acids to systematic biology and even to computer science.

The whole exercise has been great fun for the

two of us. We could hardly have dreamed where this effort would lead when we began to work together in 1981. It has been exciting to watch a technical revolution sweep through an entire area of biology. It is also gratifying and amusing to be told by colleagues at various institutions that this is one area where the plant sciences are way ahead of the animal sciences.

# INTRODUCTION

*Douglas E. Soltis,*[1] *Mark W. Chase,*[2] *and Richard G. Olmstead*[3]

During the past several years, while *rbc*L sequences were being rapidly generated, it occurred to us that an excellent opportunity existed to conduct the first in-depth molecular phylogenetic analysis of seed plants in general, and angiosperms in particular. We therefore invited the many investigators throughout the world involved in *rbc*L sequencing studies to contribute their unpublished sequences for a broad phylogenetic analysis. The responses to our inquiries were uniformly positive. The large analysis (Chase et al.), as well as the numerous companion papers, therefore attest to the spirit of cooperation in the systematics community.

We stress to readers of the large analysis that the trees presented therein should not be viewed in some absolute way as depicting "the phylogenetic relationships" among seed plants. To the contrary, numerous most-parsimonious solutions exist, and the results presented must be viewed with this cautionary note in mind. Furthermore, we do not view this exercise as an end in itself, but rather as a stimulus for directing future research into the phylogenetics of seed plants. Undoubtedly, the large analysis could benefit from more sequences (greater taxon density) as well as more sophisticated and lengthy data analyses. We also hope that the large analysis will not only help to direct future molecular investigations, but also investigations of morphological, anatomical, chemical, and cytological characters.

In conducting a phylogenetic analysis of such magnitude as the large analysis, several important points were made clear. First, it became very difficult for individual investigators to remain isolated as students of particular groups (e.g., rosids, asterids, magnoliids, etc.). For example, in the large analysis some traditional members of Rosidae appeared within an expanded Asteridae clade, and traditional Hamamelidae appeared in lineages associated with distinct groups of rosids. Thus, investigators working on supposedly distantly related groups were frequently connected as a direct result of their *rbc*L sequencing efforts. Similarly, in many instances, the taxa under investigation in one lab became suitable outgroups for studies in other labs of other groups of plants. All of these events forged new collaborations and fostered cooperation among many, perhaps most, of the numerous co-authors of the large analysis. Second, as a byproduct of this massive collaboration, many sequences became widely available, allowing those working on companion papers to sample more thoroughly than could have been done in isolation. Third, it is possible to generate sequences much more easily and rapidly than one can rigorously analyze them. That is, our molecular methodology seems to have surpassed in speed our computer-assisted means of data analysis. Clearly, future efforts should be directed toward improved and more rapid means of data analysis. Appropriate levels of time and resources need to be dedicated to the analysis of sequence data, as well as their acquisition.

To assist readers, we have put together a large appendix at the end of this issue that lists all of the taxa for which *rbc*L sequences are reported, both in the large analysis and in the companion papers. Readers should note that the companion papers often include *rbc*L sequences for additional taxa not used in the large analysis of Chase et al. It is our hope that this appendix will assist readers in rapidly determining those taxa for which *rbc*L sequences are already available. However, it is also important to keep in mind that this appendix is already out of date: the actual number of *rbc*L sequences now available is well over 1,000.

Also provided in the appendix is voucher information for the taxa for which *rbc*L was sequenced. Although the great majority of species analyzed has been properly vouchered, vouchers were unfortunately not prepared for some of the taxa for which *rbc*L sequences are reported in the papers of this issue. This may, in part, be an unfortunate consequence of the rapidly advancing DNA technology allowing amplification of genes such as *rbc*L from DNA extracted from minute amounts of leaf material. Hence, leaf material is often obtained from botanical gardens or from collectors, and suf-

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ficient material for the preparation of vouchers is often unavailable. The studies in this issue also illustrate, therefore, the critical role that botanical gardens now play as sources of living material for phylogenetic reconstruction. Unfortunately, plants grown at botanical gardens sometimes are not represented by herbarium specimens, and we would therefore urge botanical gardens to make voucher specimens for their living collections. Thus, the studies in this issue reinforce the need and importance of voucher information for all taxa used in molecular systematic studies. When vouchers are not available, the results obtained should be considered carefully, particularly in those instances in which surprising or unexpected taxonomic placements were obtained for such samples.

We hope that the large analysis and companion papers presented herein will not only act as a stimulus for future molecular and non-molecular systematic endeavors, but also will underscore what can be accomplished through the collaboration of numerous investigators. The large number of investigators cooperating in the large analysis is, as far as we are aware, unprecedented in the history of systematics. The future holds many additional opportunities for broad collaborations of similar scope as *rbc*L sequences from additional taxa and sequences of additional genes are obtained. It is our sincere hope that this issue will serve as a model and stimulus for what can be accomplished through the cooperation of numerous scientists.

We dedicate this issue to Arthur Cronquist, whose ideas and syntheses of systematic data provided inspiration, guidance, and stimulus to all botanists and whose classification provided much of the context for the papers presented. Plant systematics has benefited immeasurably not only from Arthur's hypotheses, but also from his personality and wit.

# PHYLOGENETICS OF SEED PLANTS: AN ANALYSIS OF NUCLEOTIDE SEQUENCES FROM THE PLASTID GENE *rbc*L[1]

*Mark W. Chase,*[2] *Douglas E. Soltis,*[3] *Richard G. Olmstead,*[4] *David Morgan,*[3] *Donald H. Les,*[5] *Brent D. Mishler,*[6] *Melvin R. Duvall,*[7] *Robert A. Price,*[8] *Harold G. Hills,*[2] *Yin-Long Qiu,*[2] *Kathleen A. Kron,*[2] *Jeffrey H. Rettig,*[9] *Elena Conti,*[10] *Jeffrey D. Palmer,*[8] *James R. Manhart,*[9] *Kenneth J. Sytsma,*[10] *Helen J. Michaels,*[11] *W. John Kress,*[12] *Kenneth G. Karol,*[10] *W. Dennis Clark,*[13] *Mikael Hedrén,*[14] *Brandon S. Gaut,*[7] *Robert K. Jansen,*[15] *Ki-Joong Kim,*[15] *Charles F. Wimpee,*[5] *James F. Smith,*[12] *Glenn R. Furnier,*[16] *Steven H. Strauss,*[17] *Qiu-Yun Xiang,*[3] *Gregory M. Plunkett,*[3] *Pamela S. Soltis,*[3] *Susan M. Swensen,*[18] *Stephen E. Williams,*[19] *Paul A. Gadek,*[20] *Christopher J. Quinn,*[20] *Luis E. Eguiarte,*[7] *Edward Golenberg,*[21] *Gerald H. Learn, Jr.,*[7] *Sean W. Graham,*[22] *Spencer C. H. Barrett,*[22] *Selvadurai Dayanandan,*[23] *and* *Victor A. Albert*[2]

## ABSTRACT

We present the results of two exploratory parsimony analyses of DNA sequences from 475 and 499 species of seed plants, respectively, representing all major taxonomic groups. The data are exclusively from the chloroplast gene *rbc*L, which codes for the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO or RuBPCase). We used two different state-transformation assumptions resulting in two sets of cladograms: (i) equal-weighting for the 499-taxon analysis; and (ii) a procedure that differentially weights transversions over transitions within characters and codon positions among characters for the 475-taxon analysis. The degree of congruence between these results and other molecular, as well as morphological, cladistic studies indicates that *rbc*L sequence variation contains historical evidence appropriate for phylogenetic analysis at this taxonomic level of sampling. Because the topologies presented are necessarily approximate and cannot be evaluated adequately for internal support, these results should be assessed from the perspective of their predictive value and used to direct future studies, both molecular and morphological. In both analyses, the three genera of Gnetales are placed together as the sister group of the flowering plants, and the anomalous aquatic *Ceratophyllum* (Ceratophyllaceae) is sister to all other flowering plants. Several major lineages identified correspond well with at least some recent taxonomic schemes for angiosperms, particularly those of Dahlgren and Thorne. The basalmost clades within the angiosperms are orders of the apparently polyphyletic subclass Magnoliidae sensu Cronquist. The most conspicuous feature of the topology is that the major division is not monocot versus dicot, but rather one correlated with general pollen type: uniaperturate versus triaperturate. The Dilleniidae and Hamamelidae are the only subclasses that are grossly polyphyletic; an examination of the latter is presented as an example of the use of these broad analyses to focus more restricted studies. A broadly circumscribed Rosidae is paraphyletic to Asteridae and Dilleniidae. Subclass Caryophyllidae is monophyletic and derived from within Rosidae in the 475-taxon analysis but is sister to a group composed of broadly delineated Asteridae and Rosidae in the 499-taxon study.

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Current assessments of higher-level relationships in seed plants are based largely on informed judgments of the relative value of various reproductive and vegetative characters (including secondary chemistry) and to some extent on historical precedent. Authors of recent taxonomic schemes (for example, Dahlgren, 1980; Takhtajan, 1980, 1987; Cronquist, 1981; Thorne, 1983, 1992) have synthesized an enormous amount of information. Nevertheless, their taxonomic decisions have been guided by estimations of which characters are reliable indicators of relationships. These differing judgments are responsible for radical differences in delimitation and relative ranks of taxa in each system of classification. Recently, a number of explicit, cladistic hypotheses have been developed at inclusive hierarchical levels (e.g., Crane, 1985, 1988; Dahlgren & Bremer, 1985; Dahlgren et al., 1985; Doyle & Donoghue, 1986, 1992; Bremer et al., 1987; Donoghue & Doyle, 1989; Loconte & Stevenson, 1991; Martin & Dowd, 1991; Hamby & Zimmer, 1992; Hufford, 1992; Olmstead et al., 1992; Taylor & Hickey, 1992). Such cladistic studies have previously been limited in scope; some data matrices contain significant taxonomic gaps, and in others characters for some taxa are missing. Both of these factors may have unpredictably misleading effects (Nixon & Davis, 1991; Platnick et al., 1991). Despite a great deal of investigation and analysis, seed-plant phylogenetics is, at best, in a preliminary stage of investigation and knowledge.

Molecular data, specifically DNA sequences, have received a great deal of attention as a potential source of "phylogenetically informative" characters that are putatively less ambiguous than nonmolecular characters. Such pronouncements suffer from the limitation that, at higher taxonomic levels, no extensive sampling and phylogenetic description of DNA sequence variation has taken place. The most taxonomically comprehensive analysis of nucleic acid sequences published so far on plants (rRNA; Hamby & Zimmer, 1992) used only 60 taxa, and a number of these were partial sequences. Martin & Dowd (1991), using nucleic acid sequences of the small subunit of RuBisCO (*rbc*S) inferred from amino acid sequences, studied 335 taxa from 135 families, still less than a third of angiosperm families. If insufficient sampling of taxa or characters (i.e., sequence length, acknowledged as a problem with the *rbc*S data studied by Martin & Dowd, 1991) are indeed factors, then no valid investigation of the "informativeness" of a given gene sequence exists for seed plants. Thus we are left with only an unfounded assessment of sequence data as having the *potential* to aid in estimating higher-level relationships.

Suggestions that the chloroplast gene *rbc*L, which codes for the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO or RuBPCase), was an appropriate locus to use in phylogenetic studies began with Ritland & Clegg (1987) and Zurawski & Clegg (1987). Initial attempts to evaluate relationships used only a dozen or so sequences representing all land plants (Palmer et al., 1988; Giannasi et al., 1992). Other recent studies have been restricted to single families (Doebley et al., 1990; Kim et al., 1992) or putatively closely related families (Soltis et al., 1990; Les et al., 1991; Donoghue et al., 1992; Olmstead et al., 1992; Rettig et al., 1992). Most of the latter studies began the process of incorporating significantly greater sampling to enhance their phylogenetic perspective. The use of *rbc*L was spurred by G. Zurawski, who generously made available a set of internal sequencing primers. The advent of temperature cyclers and high-temperature-resistant DNA polymerases (sometimes termed Polymerase Chain Reaction or PCR) has greatly enhanced rates at which gene sequence data are accumulating, so that effects on phylogenetic estimates of more intensive sampling of sequence variation can now be investigated.

We wish to examine here the degree to which a representative sampling of sequence variation for *rbc*L contains evidence of the evolutionary history of seed plants. In this study, we address the quality of evidence present in *rbc*L sequences for all major seed-plant lineages (roughly 265 families, the exact number depending on the taxonomic scheme followed). To a limited extent, we will compare our phylogenetic hypotheses with recent schemes, but such comparisons are difficult and must be considered heuristic because sister-group relationships ex-

from the DGAPA, Universidad Nacional Autónoma de México, Mexico, to LEE. We also thank David L. Swofford and John M. Mercer for assistance and advice in running the parsimony analyses; William S. Alverson, Michael T. Clegg, Julie Dowd, E. Allen Herre, Peter G. Martin, and James E. Rodman, for access to their unpublished sequences; Jeffrey J. Doyle, Robert F. Thorne, Peter Westin, Michael J. Donoghue, and several anonymous reviewers for their helpful suggestions; and the Royal Botanic Gardens, Kew, for support in the final stages of the preparation of the manuscript.

Footnotes 2–23 follow the Literature Cited.

pressed in cladograms are difficult to relate directly to diagrams and statements of progenitor/descendant relationships used in many taxonomic schemes. Dahlgren et al. (1985) and Dahlgren & Bremer (1985) have published analyses most similar to the ones presented here but they are not of a similar scope. Although some specific topological components can be compared to other cladistic studies (Conti et al., 1993; Rodman et al., 1993; Qiu et al., 1993; and several of the other studies in this issue), morphological phylogenetic studies at this level with similar, broad taxonomic sampling do not exist. The computational difficulties of evaluating internal support (e.g., the bootstrap, Felsenstein, 1985; decay analysis, Bremer, 1988) or departure from matrix randomness (Archie, 1989; Faith & Cranston, 1991; Källersjö et al., 1992) for such large numbers of taxa likewise prevent us from addressing extensively these issues here. We do present an analysis of families traditionally referred to Hamamelidae as an example of how internal support for specific clades might be examined. (See also other papers in this issue that address internal and external support for subsets of the general results.) Thus, the broad relationships described here can be used to focus more restricted (with fewer taxa), and therefore more rigorous, investigations.

We expect that patterns presented here will change somewhat as sequences of more species are added or if methodological improvements permit exact solutions (for a discussion of progress, see Penny et al., 1992). These results nonetheless have great value, both from heuristic and methodological perspectives, although the preliminary nature of these studies precludes a detailed examination of implications for seed-plant taxonomy and character evolution, as well as investigations of gene and protein evolution.

We have generally followed the taxonomic circumscriptions of Cronquist (1981) for dicots because this system conforms closely to those used in most textbooks and floras. For monocots, we have adopted the system of Dahlgren et al. (1985) but have changed the superorder ending "-iflorae" used by Dahlgren to the more appropriate "-anae" (Thorne, 1992).

## Materials and Methods

Selection of taxa for this study was not guided by a specific plan. Close examination of genera included in the analysis will reveal an uneven taxonomic distribution; some groups are well represented (e.g., Asteraceae and Asteridae in general, Cornaceae, Ericales, Magnoliaceae, Zingiberanae), whereas others are poorly sampled (e.g., dilleniid orders, especially Violales and Theales). Despite lack of a coordinated effort, all subclasses and orders have at least some representatives. All species that are used in this issue of the *Annals of the Missouri Botanical Garden* are listed alphabetically by family in a final Appendix along with other information concerning voucher status, sequence gaps, literature citations for published sequences, and figures of this paper in which each taxon occurs. Some taxa that were included in the 475-taxon data set were excluded from the 499-taxon matrix. Thus, in the second analysis certain families have fewer representatives, but the overall representation of lineages is greater.

Due to the large number of laboratories that contributed unpublished sequences, no standardized procedure was used to produce the sequences analyzed here. A generalization would be the following: a fragment containing *rbc*L was amplified from a total DNA extract using primers that flank or are near the ends of the coding region; this fragment was then directly sequenced using one of several different procedures or was cloned using standard recombinant DNA techniques; dideoxy sequencing generally included both strands for at least ⅘ of the minimally 1428-bp gene. Some workers used more closely spaced primers to sequence only one strand of DNA; either strategy appears to provide reasonably error-free sequences. Most extraction protocols relied on fresh or freshly dried leaf samples, but some samples were amplified from DNA extracted from herbarium specimens as old as 20 years.

Amplification of *rbc*L from some taxa produced two different products. Some of these products were different enough in size to observe on an agarose gel, whereas others were detected initially because multiple bands occurred at the same points in autoradiograms, indicating that more than one template was present. Nearly all cycads produced two loci (Hills & Chase, unpublished), which were separately cloned and sequenced to characterize both copies. In cycads examined, one copy contained deletions that disrupted the reading frame, an indication that this copy may represent a "pseudogene." In Convolvulaceae, Olmstead (unpublished) detected two copies of *rbc*L, one copy of which contained deletions. In *Canella* (Canellaceae; Qiu et al., 1993) and *Galphimia* (Malpighiaceae; M. W. Chase, H. G. Hills & W. R. Anderson, unpublished), two size-conserved copies of *rbc*L were also encountered. In *Galphimia*, one copy clearly contained substitutions at numerous sites otherwise conserved among angiosperms, suggesting that this

copy was a pseudogene. In *Canella*, no such unusual substitutions were observed in either copy. Two, reading-frame-intact copies of *rbc*L are also reported in Ulmaceae (E. Conti & K. J. Sytsma, unpublished). For *Canella*, we included both sequences in all analyses, but because the two sequences are always each other's sister we show only the position of "*Canella*" (in fact, there are two terminals here; the complete matrix used in Search II thus has 500 terminals but only 499 taxa).

Sequences of *rbc*L were easily aligned by sight. Among land plants, the coding region contains little size variation through base position 1428 (numbered from the first nucleotide of methionine in the start codon, AUG). Positions 1426, 1427, and 1428 are the most common stop-codon among land plants; longer reading frames, up to 1452 in some monocots and 1458 in the Asteraceae (Kim et al., 1992), appear to be due to insertions, often of a short repeating sequence. Most laboratories have sequenced past this codon, but for phylogenetic analysis we have terminated all sequences at position 1428 to be confident that we have analyzed homologous regions (the portion of the gene included in this analysis for each species is also included in the Appendix). All sequences were entered into a text file in NEXUS format (used by PAUP 3.0; Swofford, 1991) as complete sequences and then analyzed directly in nucleotide form. Matrices used in both searches are available from the first author upon receipt of request and a diskette for each matrix.

## TREE-SEARCH STRATEGY

Parsimony-based methods permit direct examination of hypothesized character-state changes on the reconstructed tree, and this information can be used in studies of molecular evolution. (These are, however, likely to be underestimates of sequence change and could be misleading for this reason.) Numerous empirical studies have shown that not all classes of substitutions are equally likely, and this kind of information may be incorporated into weightng schemes for nucleotide data (Swofford & Olsen, 1990; Albert & Mishler, 1992; among others). Various models of molecular evolution exist, and appropriately circumspect use of these may assist in the separation of historical signal from homoplasy. The character-state weighting model of Albert et al. (1993, this issue) uses probability formulae to calculate weights for different classes of molecular change. We have used their method in the 475-taxon analysis presented here. Although the assumptions of the Albert et al. model are admittedly simplistic, we nonetheless support the investigation of weighting approaches to nucleotide data and view the model used here as a justifiable first approximation. It must be recognized that giving all categories of molecular change equal transformational weight is also an assumption, but one that the investigation of Albert et al. (1993) found to be adequate if sampling effects were not a factor. Actual weights applied in this study fall within such a narrow and minimally asymmetrical range that deviation of results from those using the "equal weighting" criterion of Fitch (1971) is likely to be slight (see Albert et al., 1993).

Recently, concern has focused on the probability that "islands" of equally parsimonious trees exist, particularly in large data sets (Maddison, 1991). Because of their enormous size, our analyses do not use methods of multiple random taxon-addition, which have been suggested to uncover such disjunct, equally optimal islands. This topic is addressed in most empirical papers in this number.

The search for parsimonious trees consisted of several separate but linked heuristic searches using either PAUP 3.0r (**Search I**; 475 taxa) or 3.0s (**Search II**; 499 taxa). All searches included the full data matrix (all codon positions). Search I was performed on a SPARC II (Sun, Inc.) workstation (PAUP 3.0 for non-Macintosh computers is available only by special arrangement with D. Swofford). For Search II, a Macintosh Quadra 800 with 20 MB RAM was used. (Although slower than a Sun computer, the more interactive nature of a search on a PC is preferred by many workers.)

In **Search I**, an initial heuristic search with character-state changes given equal weight (i.e., "unordered" status), SIMPLE data addition sequence, STEEPEST DESCENT, and NNI (nearest-neighbor interchange) branch swapping algorithm was used to find a single tree (MULPARS option deactivated). The second phase used this single tree obtained from phase one as a starting tree for another heuristic search, this time using the SPR (subtree pruning-regrafting) branch swapping algorithm with MULPARS deactivated again. The third phase paralleled the first and second; the single SPR tree from phase two was used as the starting topology for a heuristic search using the TBR (tree bisection-reconnection) branch swapping algorithm, again with MULPARS deactivated.

The fourth phase used the single TBR tree as the starting point for a heuristic search employing a character-state weighting criterion (with a different step matrix for each codon position; cf. Swofford, 1991; Albert & Mishler, 1992; Albert et al., 1993). This time MULPARS was activated.

Transversion substitutions were weighted over transitions differentially by codon position (Albert et al., 1993). The specific weights used were the following: for transitions, 5520 (first positions), 6368 (second positions), 4039 (third positions); for transversions, 6620 (first positions), 7470 (second positions), 5127 (third positions). These weights were calculated from empirically derived parameters (see Albert et al., 1993, for a complete description and justification). Because use of step matrices is CPU-intensive, this search was executed with the simplest branch-swapping algorithm, NNI. Additionally, because of dynamic RAM limitations (a tree of 475 terminals occupies a great deal of memory), we restricted our search to a maximum of 500 trees. Although the initial TBR tree was by default a member of a single island, we hoped to provide a bridge to shorter trees through use of the STEEPEST DESCENT option (see Maddison, 1991; Swofford, 1991). This final step yielded 500 equally parsimonious, weighted trees. Because the maximum prespecified number of trees was found, many others probably exist at the same length. Search I required approximately 200 hours to complete.

**Search II** was performed for three reasons. First, the likely existence of other islands of equal or greater parsimony prompted us to use a strategy that would be more likely to find shorter trees and perhaps a different topology. Second, we were concerned about the effects of the Albert et al. (1993) weighting scheme upon the resulting topology. Third, we wished to examine positions of additional taxa (and make use of updated sequences) that became available after Search I was completed; many of these belonged to previously unrepresented lineages. Differences between these two sets of trees could thus be due to different taxon sampling, corrections or completions of sequences after Search I was finished, or search strategy. We did not intend these two searches to be controlled, direct tests (i.e., with only one variable differing between them); we show them both, rather than simply the one that we judge to be better (Search II), because their similarities, despite variation in taxon composition and search strategy, are considerable. They each represent results of searches that in their own context are worthy of publication, and their differences should be viewed as reasons to be skeptical of both and as cause for future study with more *rbc*L data as well as other characters.

In Search II, we were able to save more trees at the shortest length found: 3,900 rather than only 500 trees. The initial starting tree was produced by using the CLOSEST addition sequence with the HOLD option set for five trees (this in effect permitted initial swapping on several different starting topologies). Approximately 120 hours were required merely to add all taxa in this manner. The initial search (i) used NNI swapping and STEEPEST DESCENT with MULPARS off. The shortest single tree found was then swapped on using (ii) TBR, which generally found a shorter tree, at which time (iii) NNI (with MULPARS) was used. When use of MULPARS resulted in 3,900 trees, which used up available RAM, a single tree was randomly selected (iv) to swap on with TBR (MULPARS off). If this resulted in a shorter tree being found, the search was then stopped and restarted (iii, again) using NNI and MULPARS and this shorter tree as starting point (iii and iv were repeated until no shorter trees were found). The shortest tree length found with this method was 16,305. Three randomly selected trees from the 3,900 saved at this length were swapped in succession to completion with TBR (no MULPARS), and no shorter trees were found. A strict consensus tree was computed, and branch lengths for one randomly selected tree were calculated using the ACCTRAN optimization. Search II thus used no relative weighting; it required approximately four weeks to complete.

## Caveats

Methodologically, these searches suffer from (i) uncertainty about maximum parsimony, (ii) unquestionable absence of many trees at the same level of optimality, (iii) identification of only a single topology, and (iv), in Search I, incomplete branch swapping on any of the shortest trees found. We would never recommend these search strategies for smaller data sets, but several options were seriously restricted by the number of taxa included (these are reputedly the largest PAUP analyses attempted to date). Specific sections of the general topologies, when analyzed in a more "localized" manner, provide different sets of relationships (see Michaels et al., 1993; Morgan & Soltis, 1993; both this issue). The broader taxon distribution of the general analysis (thus with far greater outgroup information) may be assessing character-state change on the immediate branch leading to a specific ingroup differently than in more restricted analyses. Greater outgroup information could "improve" the ingroup analysis or add spuriousness to it; it is generally best to implement tree searches both with and without outgroups to examine their effects. If more restricted analyses differ from those pre-

sented here, we would certainly favor the former because of increased confidence in finding parsimonious solutions. We nonetheless view these analyses as instructive about seed-plant relationships and the utility and limits of *rbc*L information (see Discussion).

The major limiting factor in our studies is clearly matrix size. When confronted with the largest molecular database relevant to seed plants, computational trade-offs inevitably arose. The amount of time spent on these approximations may not be directly proportional to the time taken to generate all the *rbc*L sequences, but no method exists to predict how many trees at how many steps shorter might have been found after additional months or even years of continuous computation. We have opted for the approximations presented here rather than commit ourselves to an open-ended experiment.

Potential effects of errors in autoradiogram reading and data entry should be considered. We detected a number of internal stop-codons in sequences used in these analyses, and other workers have reported errors of various kinds. Most of these were corrected in the matrix used in Search II. Certainly the potential for errors is present, but the effects of such mistakes should not be extensive because they are likely to be random.

Identification of some taxa in this analysis has been questioned due to peculiarity of placement. One example of this has been now identified among the species used in Search I. We have not expunged it from the illustrations; the results represent the outcome of real tree searches and are instructive for that reason. The sequence analyzed was an actual member of the clade into which it was placed, but it was not the species to which it had been attributed. The material sent by a botanical garden and labeled as *Kirengeshoma* was evidently misidentified. It was almost certainly a member of the *Parnassia* group (Saxifragaceae sensu lato; the position it occupies in Fig. 11A) rather than a member of Hydrangeaceae. Sequencing of another specimen of *Kirengeshoma* and subsequent data analysis revealed the expected placement of this genus with other Hydrangeaceae (Xiang & Soltis, unpublished). Other "surprising" results also have been checked by obtaining another sample of the taxon in question and re-sequencing *rbc*L. The original sequence of purportedly saxifragaceous *Montinia* (which nested in Solanales) was checked and found to be accurate. Still others (such as *Sargentodoxa* among Fabaceae) are still being reassessed. Most workers have tried to make vouchers for each species in this study (see Appendix). Many tissue samples were provided by botanical gardens, and, if vouchers are not included with samples, investigators are dependent upon identification of these plants by the respective organizations (see Goldblatt et al., 1992; it is critical that a voucher sample taken from the same plant used for DNA extraction be included at the time of collection; accession numbers or vouchers taken previously are subject to later events, such as lost labels or collector mistakes). Because a number of the samples used in these two analyses are unvouchered (see Appendix), reproducibility is compromised. In cases with multiple species from a family, we should be able to recognize grossly misidentified samples (but this is true for only 37% of the 265 families represented).

## Results

For display purposes, we show here the combinable component consensus (Bremer, 1990) of the 500 equally parsimonious trees found in Search I (Figs. 1–15, A series). Because these are character-state weighted trees, tree lengths and tree statistics (e.g., consistency index, etc.) are not comparable to those of Fitch trees and are not given here. For Fitch trees found in Search II, the length was 16,305 with a consistency index (C.I., excluding unique substitutions and constant characters) of 0.102 and a retention index (R.I.) of 0.632. The branch lengths, again with ACCTRAN optimization, are shown on one of the 3,900 trees selected at random (Figs. 1–15, series B). Branches that collapse in the strict consensus tree are indicated by arrows on the B series (Figs. 3–15B).

First we will summarize the topology found in Search I ("A" series of figures). The results of Search II ("B" series) have been interdigitated with those of Search I to facilitate comparisons. After describing the results of Search I, we briefly examine major differences between the two results. Note that all figures in the A series are from the combinable component consensus tree, whereas in the B series, Figures 1B and 2B are the strict consensus tree (branch lengths in Fig. 2B, however, were taken from a single tree) and the remainder (Figs. 3B–15B) are a single tree randomly selected from 3,900 equally parsimonious Fitch trees (this may be confusing; for example, whereas the polytomy among monosulcate clades in Figs. 1B and 2B is due to variation among the 3,900 trees for branches in this portion, the topology shown in 3B is resolved because it is resolved in the single tree selected). To indicate branches of the B series that are absent in the strict consensus tree of the 3,900,

we have placed arrows to their right. The branch lengths presented in the B series should under no circumstances be interpreted as meaningful measures of support; thus, in the example of Hamamelidae provided, branches that decay at one step less parsimonious have lengths that range from 2 to 16 steps, whereas those that decay at four steps less parsimonious range from 7 to 14 steps (Fig. 16). The sole reason for providing branch lengths in the B series is to permit readers to estimate roughly relative degrees of divergence and to identify cases in which long terminal branches are connected to short internal branches (a situation in which adding related taxa often radically alters hypothesized relationships).

**Search I**. Unless stated otherwise, we have used the taxonomic circumscriptions of Cronquist (1981) for dicots and Dahlgren et al. (1985) for monocots, although we acknowledge that other recent systems fit these results better. We arranged the unrooted trees of both searches with cycads sister to all other seed plants (Figs. 1–3) in accord with recent results of several non-molecular cladistic studies (Crane, 1985, 1988; Doyle & Donoghue, 1986, 1992). In Search I, conifers are paraphyletic, but some trees (not shown) found in Search II have a monophyletic conifer lineage; the strict consensus tree from Search II is unresolved regarding conifers (Figs. 1B, 2B; we have cited in this section the B series of figures along with the A series if they include the same general set of taxa). The three genera of Gnetales, *Ephedra*, *Welwitschia*, and *Gnetum*, are highly divergent from all other seed plants but were nonetheless identified as sister of the angiosperms (Fig. 3A, B), within which *Ceratophyllum* (Ceratophyllaceae) alone is sister to and highly divergent from the rest (Fig. 4A, B). The major feature of flowering plants (exclusive of *Ceratophyllum*) is their separation into two major groups; these correspond well with distributions of the two major angiospermous pollen types, uniaperturate (monosulcate and monosulcate-derived) and triaperturate (tricolpate and tricolpate-derived). *Ceratophyllum* has inaperturate pollen (Cronquist, 1981). The major exception to this split is the presence of tricolpate pollen in Illiciaceae and Schisandraceae, which fall among the monosulcate taxa (Fig. 4A, B; see Qiu et al., 1993, this issue). No morphological support for monophyly of the monosulcate clade has been recognized in the literature (their pollen type exists among nonflowering seed plants and thus must be considered plesiomorphic).

Three monophyletic lineages within uniaperturate magnoliids were identified, and these correspond closely, although not exactly, to (i) Magnoliales, (ii) Laurales, and (iii) "paleoherbs" (here defined as composed of Aristolochiales, Piperales, and Nymphaeales; Fig. 4A). Monocots (also with uniaperturate pollen and sometimes included in "paleoherbs"; Donoghue & Doyle, 1989) represent a fourth member of this clade. Among the paleoherbs are also nested several problematic families: Illiciaceae, Schisandraceae (both Illiciales), Amborellaceae (Laurales), and Austrobaileyaceae (Magnoliales). Chloranthaceae are also allied cladistically with the paleoherbs, but *Chloranthus* does not form a monophyletic group with other Piperales.

Monocots are a well supported monophyletic group (see Duvall et al., 1993, and Qiu et al., 1993, both this issue) and are derived from within monosulcate Magnoliidae; the paleoherbs are their immediate sister group (Fig. 4A). Within monocots (Fig. 5A, B), Aranae plus *Pleea* (of polyphyletic Melanthiaceae; Lilianae) are basal-most, followed by Alismatanae plus *Burmannia* (Burmanniaceae) and *Aletris* (Melanthiaceae). Lilianae form a paraphyletic series of three lineages that correspond well to Dioscoreales, Liliales, and Asparagales of Dahlgren et al. (1985), except in the placement of certain families (Iridaceae, Orchidaceae, and Smilacaceae) and genera (*Chamaelirium* of Melanthiaceae: Melanthiales). *Vellozia* (Velloziaceae: Bromelianae), *Freycinetia* (Pandanaceae: Pandananae), and *Sphaeradenia* (Cyclanthaceae: Cyclanthanae) together form a monophyletic clade that is collectively sister of the Liliales. The "commelinoid" group of monocots (Fig. 6A, B) incorporates all of those that Harris & Hartley (1980) found to exhibit fluorescing cell-wall phenolics. In both searches, this commelinoid clade includes monophyletic Arecanae and Zingiberanae and polyphyletic Bromelianae and Commelinanae (Fig. 6A, B). Cyclanthaceae have the same phenolic biosynthetic pathway but do not accumulate end products; they are not members of the commelinoid assemblage (Clark et al., in prep.).

The two orders of Magnoliidae with triaperturate pollen, Ranunculales and Papaverales, form a clade that is sister to the rest of "eudicots" (Fig. 7A, B). The term "eudicot" has been variously defined in the literature, but we use it here to refer to all angiosperms with triaperturate or triaperturate-derived pollen (Donoghue & Doyle, 1989; Doyle & Holton, 1991). This is one of the best supported clades among angiosperms (Qiu et al., 1993, this issue). Two other basal clades within the eudicots (Fig. 7A, B) consist of some Hamamelidae (Trochodendraceae and Tetracentraceae) and Platanaceae, Sabiaceae, Nelumbonaceae, and Proteaceae.

Within eudicots, two large sister clades are iden-

tified, one that corresponds roughly to Asteridae and the other to Rosidae (Figs. 1, 2). Membership in both lineages is considerably expanded with respect to their circumscription by Cronquist (1981), although less so with respect to the circumscriptions of Dahlgren & Bremer (1985) and Thorne (1992). These two major clades (Fig. 2A, B) reflect the division of eudicots into two major groups (Young & Watson, 1970): sympetalous/tenuinucellate and polypetalous/not tenuinucellate (asterids and rosids, respectively, in our figures). The "crassinucellate" condition actually consists of several different states. Exceptions to this generalization exist, but these traits appear much less homoplastic here than in most systems of classification. The basalmost lineage within Rosidae includes Saxifragaceae sensu stricto and Crassulaceae besides lower hamamelids such as *Cercidiphyllum* and *Hamamelis* (Fig. 8A; see Morgan & Soltis, 1993, this issue, for a discussion of Saxifragaceae sensu lato). The next-most-basal group contains Caryophyllidae (including Plumbaginaceae and Polygonaceae; Rettig et al., 1992) plus Droseraceae, Nepenthaceae (Nepenthales, Dilleniidae; see Albert et al., 1992b), Dilleniaceae (Dilleniidae), and Vitaceae (Fig. 9A).

The remaining Rosidae are split into two large sister groups (Figs. 2A, 10A, 11A). In one (rosid I) are several families of higher Hamamelidae, Euphorbiales, Fabales, Linales, Polygalales, and Rosales (Fig. 11A). Other members of this clade include a number of dilleniid families: Ochnaceae (Theales), Datiscaceae, Passifloraceae, and Violaceae (all Violales). Ordinal boundaries of this group of Rosidae (sensu Cronquist, 1981) are largely unsupported; this assemblage is particularly heterogeneous. The largest polytomy in the consensus tree from Search I occurs at the base of this group, and sampling of the families that potentially belong to this clade is the most sparse in this analysis. The other major lineage of Rosidae (rosid II; Fig. 10A) includes orders Myrtales (see Conti et al., 1993, this issue) and Sapindales, for which ordinal boundaries are reasonably intact. Malvaceae (Malvales; Dilleniidae) and all but one of the mustard-oil families (those in Capparales plus others in Dilleniidae; see Rodman et al., 1993, this issue) are associated with Sapindales. Geraniaceae are also members of this clade, although other members of Geraniales appear elsewhere (Oxalidaceae with a group of families in Rosales, Fig. 11A; Balsaminaceae with Ebenales, Fig. 13A, B; and mustard-oil-producing Limnanthaceae and Tropaeolaceae with Capparales, Fig. 10A, B; Price & Palmer, 1993, this issue). Two members of Rosales, *Greyia* (Greyiaceae) and *Francoa* (Saxifragaceae), appear derived from within Geraniaceae, if *Viviania* is included in Geraniaceae (see also Price & Palmer, 1993, and Morgan & Soltis, 1993, this issue).

The tenuinucellate/sympetalous clade that terminates in Asteridae sensu Cronquist (1981) was also identified by Olmstead et al. (1992) in their efforts to circumscribe subclass Asteridae using *rbc*L sequences. This study greatly expands upon their sampling and identifies as members of the asterid clade two lineages of often polypetalous Rosidae (Figs. 2A, 12A): (i) Santalales plus Paeoniaceae and Gunneraceae and (ii) some families of Cornales plus Hydrangeaceae (see Xiang et al., 1993, this issue). The sister group of Asteridae is a clade (Figs. 2A, B, 13A, B; see Kron & Chase, 1993, this issue) that contains the dilleniid orders Ebenales, Ericales, Primulales, Diapensiales, plus some members of Theales (Actinidiaceae and Theaceae). Sarraceniaceae (Nepenthales; Dilleniidae) and *Roridula* (but not *Byblis* of Byblidaceae of Rosales: Rosidae) are also members of this lineage (Albert et al., 1992b). Polemoniaceae (Solanales: Asteridae) and Balsaminaceae (Geraniales: Rosidae) also belong to this ericalean/ebenalean group. (See also Olmstead et al., 1993, this issue, for a treatment of the Asteridae sensu lato.)

Asteridae sensu Cronquist split into two major sister groups. In one of these (asterid II; Fig. 14A, B) are families of Asterales, Calycerales, Campanulales, Dipsacales, and some Solanales (Menyanthaceae). Rosid taxa that are members of this clade include Apiales, Aquifoliaceae (Celastrales), some Cornaceae (Cornales), Pittosporaceae and Grossulariaceae (both Rosales). In the other major clade (Fig. 15A, B) fall orders Callitrichales, Gentianales, Lamiales, Rubiales, Scrophulariales, and most Solanales, although these ordinal limits are not always supported (see Olmstead et al., 1993, this issue). In this clade (Fig. 15A, B) is a group that includes rosids *Aucuba* (Cornaceae: Cornales) and *Garrya* (Garryaceae: Cornales) and hamamelid *Eucommia* (Eucommiaceae: Eucommiales), all of which accumulate aucubin (Cronquist, 1981) and share distinctive anatomical wood characteristics (E. Wheeler, pers. comm.). Thus the suite of floral characteristics that have been interpreted as support for the monophyly of Asteridae sensu Cronquist (1981) appears either (i) to have twice arisen independently from ancestors with rosalean and cornalean floral traits or (ii) to have undergone reversals in groups traditionally included in Rosidae (sensu Cronquist; Donoghue et al., 1992; Olmstead et al., 1992, 1993, this issue).

**Search II.** A number of taxa from Search I were removed from Search II (all marked with a "†" in the A series of figures) to accommodate the representatives of additional lineages in Search II.

Most of the removed taxa were from monophyletic families in which six or more species were present in Search I (for example, Asteraceae, Ericaceae sensu lato, Magnoliaceae, and Poaceae). Two others, *Burmannia* (Burmanniaceae) and *Hydrolea* (Hydrophyllaceae), were removed because they are highly sequence divergent from all other taxa; in separate, smaller analyses, these two appear to be involved in "branch attractions" and attach in radically different positions as other taxa are added or removed (other similarly divergent genera, for example, *Paeonia* and *Gunnera*, do not cause these problems and were kept; we admit to being relatively arbitrary in removing only these two taxa). *Burmannia* presents an interesting case. Members of Burmanniaceae are often achlorophyllous; in spite of being green, *Burmannia* may still derive a great deal of its nutrition through its mycorrhizal associate. In such cases in other families, a number of protein loci exhibit higher rates of sequence divergence (as measured by relative branch lengths when compared to completely autotrophic members of their lineages; C. dePamphilis, pers. comm.). Thus the high levels of sequence divergence, which make it difficult to place these taxa accurately, are a product of or at least associated with their partial heterotrophy.

For Search II, additional taxa were available (these species are marked with asterisks in the B series of figures). The placements of these are described first, and then different arrangements of taxa included in both searches are identified (the clades involved with major shifts of position are marked with an "§" in Fig. 2B). This last section describes only the major shifts of position, but many "minor" shifts also occur within clades (for example, 12 "minor" shifts take place among the taxa in Fig. 15, a clade in which only a few new species were added). What constitutes a "major" versus a "minor" alteration is, of course, a matter of personal perspective. We would therefore advise readers to examine carefully the trees from both searches for taxa of specific interest, which is one reason we presented and intercalated the results of both analyses.

*Positions of additional taxa.* *Ginkgo* (Ginkgoaceae) intercalates between cycads and conifers (Figs. 1–3B). *Taxus* (Taxaceae), *Cephalotaxus* (Cephalotaxaceae), and *Sciadopitys* (Taxodiaceae or in its own family) are members of the non-Pinaceae clade of conifers, with *Sciadopitys* sister to the rest of that clade (Fig. 3B). Within magnoliid angiosperms, *Lactoris* (Lactoridaceae) is sister to *Aristolochia* (Aristolochiaceae). Other new magnoliid species added in Search II represent additional members of families already present in Search I, and all of these form monophyletic units with other members of their respective families (Fig. 4B).

Sister to all other monocots is *Acorus* (Araceae; see Duvall et al., 1993, this issue). *Calochortus* (Calochortaceae) is sister to Liliaceae, *Hemerocallis* (Hemerocallidaceae) is sister to *Chlorophytum* (Anthericaceae), and *Lomandra* (Dasypogonaceae) is a member of the often arborescent clade composed of Agavaceae, Asphodelaceae, and Xanthorrhoeacae within Lilianae (Fig. 5B). Additional members of families in Search I are all placed as sister taxa to their respective family representatives. Among the commelinoid clade identified in Search I (Fig. 6A, B) are the following additional families: *Sparganium* (Sparganiaceae) sister to *Typha* (Typhaceae) and *Lachnocaulon* (Eriocaulaceae) among the graminoids.

Among eudicots (Fig. 7A, B), *Pachysandra* (Buxaceae) is sister to Trochodendrales (*Trochodendron* and *Tetracentron*). Composition of the various rosid clades is somewhat different in Search II (Fig. 2B; see below), but the following additional taxa are placed roughly among the rosid II (Fig. 10B) clade identified in Search I: *Shorea* (Dipterocarpaceae), *Theobroma* (Sterculiaceae), *Tilia* (Tiliaceae), and *Bombax* (Bombacaeae) are members of a malvalean clade (represented only by *Gossypium* in Search I). *Akania* (Akaniaceae) and *Bretschneidera* (Bretschneideraceae), both Sapindales, are members of the mustard-oil clade. Three additional members of Capparaceae, *Cleome*, *Koeberlinia*, and *Setchellanthus*, along with *Capparis*, create a polyphyletic Capparaceae (Fig. 10B; see also Rodman et al., 1993, this issue). *Hypseocharis* (Oxalidaceae) is sister to a clade containing many Geraniaceae (Fig. 10B; see Price & Palmer, 1993, this issue). Among members of rosid I (Fig. 11B, C) are representatives of the following new families: *Reinwardtia* (Linaceae) is sister to *Viola* (Violaceae); *Sargentodoxa* (Sargentodoxaceae) is imbedded in Fabaceae; *Humulus* (Cannabinaceae), *Trema* (Ulmaceae), and *Boehmeria* (Urticaceae) fall into an urticalean clade with *Morus* and *Ficus* (both Moraceae), but Ulmaceae are paraphyletic to Cannabaceae; *Coriaria* (Coriariaceae), *Begonia* (Begoniaceae), and three genera of Cucurbitaceae are placed with Datiscaceae; *Betula* (Betulaceae) and *Carya* (Juglandaceae) are members of the clade containing Fagaceae and Casuarinaceae; *Mouriri* and *Osbeckia* (Melastomataceae), *Punica* (Punicaceae), *Trapa* (Trapa-

ceae), and *Heteropyxis* (Myrtaceae) are members of a clade of (mostly Myrtales) that includes Onagraceae and Combretaceae (Fig. 11C). In asterid lineages, two additional families have been added: *Byblis* (Byblidaceae) and *Vahlia* (Saxifragaceae) are placed among Schrophulariales (Fig. 15B).

*Changes in placements of major clades.* At higher levels among the seed plants, Search II produced relatively few "major" differences in taxon placements from the topology of Search I. The conifers in some, but not all, 3,900 trees are monophyletic. Piperales–Aristolochiales were sister to all monosulcate angiosperms (Figs. 2B, 4B). The "paleoherb" clade of Search I (Fig. 4A) was thus split in two with the portion containing Chloranthaceae, Illiciales, Austrobaileyaceae, Amborellaceae, and Nymphaeales situated as sister to Magnoliales. Although these may seem to represent major shifts, extremely short branches separate these clades (Fig. 4B); thus neither topology has much internal support (Qiu et al., 1993, this issue). Within monocots, only shifts among the groups in Aranae, Alismatanae, and Lilianae occurred (Fig. 5B): Aranae (minus *Acorus*) are sister to Alismatanae; the clade containing Pandanaceae, Cyclanthaceae, and Velloziaceae is isolated and no longer sister to Liliales, and Dioscoreales are sister to the commelinoid taxa (the position of Asparagales in the trees from Search I). Among commelinoid taxa (Fig. 6B), *Stegolepis* (Rapateaceae) is sister to Bromeliaceae, Typhales are sister to Juncaceae–Cyperaceae, and *Flagellaria* is sister to the other graminoid clade.

Among eudicots, three major shifts of taxa present in Search I occurred. The first series of rearrangements involves the heterogeneous asterid V clade (Fig. 12A). *Gunnera* (Gunneraceae) intercalates as an isolated lineage (Fig. 7B) between Trochodendrales (plus *Pachysandra* of Buxaceae) and higher eudicots (asterids, caryophyllids, and rosids). Santalales, *Phoradendron* (Viscaceae), *Schoepfia* (Olacaceae), and *Osyris* (Santalaceae) become sister to Caryophyllidae–Droseraceae–Nepenthaceae (Fig. 9B), and this larger caryophyllid clade is shifted from a position within the rosid clade (rosid III; Figs. 2A, 9A) to sister to the larger asterid–rosid clade (Figs. 2B, 9B). The remaining member of asterid V, *Paeonia* (Paeoniaceae), is deeply imbedded within rosid III clade (Fig. 8B) as sister to Crassulaceae. We attach little significance to these shifts of position; internal branches of these groups are among the shortest supporting positions of major clades.

The second series of shifts occurs within rosids. Families of Myrtales (plus *Qualea* of Vochysiaceae, Polygalales) and the clade containing *Viviania*, *Wendtia* (both Geraniaceae), *Greyia* (Greyiaceae), and *Francoa* (Saxifragaceae) are shifted from rosid II to rosid I (Fig. 11B, C), and relationships of intermediate-level clades (containing several families, i.e., those of Urticales, Fagales, etc.) are somewhat modified from their position in Search I.

The third shift involves the two taxa that were sister to the expanded caryophyllid clade from Search I (Fig. 9A): *Dillenia* (Dilleniaceae) and *Vitis* (Vitaceae), which become sister to the rest of the larger asterid clade (Fig. 12B; *Vitis* and *Dillenia* in a sense exchanged positions with Santalales). Again, these groups have short internal branches, and these shifts would require little change of overall parsimony.

In several instances, the topology of Search II (which we favor because it was a more complete search) is more similar to that found in investigations of restricted nature (for example, outgroup relationships of Asteraceae are identical with those found by Michaels et al., 1993, this issue, and Olmstead et al., 1992, whereas those of Search I deviated in several ways).

## Discussion

Although *rbc*L sequences for several groups of spore-bearing plants are available (true mosses, hornworts, liverworts, *Equisetum*, *Isoetes*, *Lycopodium*, *Psilotum*, and both eu- and leptosporangiate ferns), their use as outgroups is complicated by extensive sequence divergence relative to that in the seed-plant ingroup. No other extant lineages of land plants are likely to have shared a common ancestor with seed plants for well over 350 million years, and a great deal of sequence change, much of it in the form of multiple, unrecoverable substitutions, has occurred. Analysis of these other land plant sequences produces topologies (not shown, but see Hamby & Zimmer, 1992, for similar results) that are radically different from all previous hypotheses of relationships (e.g., Bremer et al., 1987). In contrast, seed-plant relationships presented here are at least congruent in gross aspect with comparable morphological studies (Crane, 1985, 1988; Doyle & Donoghue, 1986, 1992; Loconte & Stevenson, 1991). Addition of highly sequence-divergent outgroups could be expected to increase ingroup homoplasy with unpredictable topological results (Felsenstein, 1978). In these analyses, we have chosen to use the more conservative approach of an unrooted ingroup analysis

of seed plants, which are almost certainly monophyletic (Doyle & Donoghue, 1986, 1992).

Likewise, effects of missing groups upon topologies may be profound (Donoghue et al., 1989) and unpredictable, and we expect the absence of the numerous extinct lineages of early land plants in molecular data matrices to pose potentially serious problems for elucidating relationships of extant lineages. Perhaps more conservative genes sampled for more of the sequence variation present within extant groups may be able to "bridge" gaps caused by extinction. Features of genome organization (such as gene and intron content and gene order; Downie & Palmer, 1992; Raubeson & Jansen, 1992) may offer more robust hypotheses than gene sequences for such questions, but these are likely to be too few to provide a fully resolved tree by themselves. A great deal more experimentation with combined data sets of morphological and molecular characters is obviously needed, and a number of these studies are underway (both with *rbc*L and rRNA/rDNA data). Consideration of these problems here is premature.

Sister-group status of angiosperms and Gnetales (Figs. 2A, B and 3A, B) is corroborated by other cladistic studies (Crane, 1985, 1988; Doyle & Donoghue, 1986, 1992; Loconte & Stevenson, 1991). The isolated position of *Ceratophyllum* as sister to all other angiosperms has been argued previously (Les, 1988; Les et al., 1991). In studies by Qiu et al. (1993, this issue) in which nonflowering seed plants were removed, this arrangement was made equivocal by the existence of another equally parsimonious island in which *Ceratophyllum* occurred in a radically different position. Hamby & Zimmer (1992; rRNA) also found a yet different placement for *Ceratophyllum* (but we suspect that the sparser sampling of their study may be responsible for most of the differences from those found with *rbc*L). In instances in which a taxon's morphology and anatomy are as divergent and potentially modified as those of *Ceratophyllum*, its position becomes difficult to address adequately in cladistic studies. *Ceratophyllum* has been absent from many morphological cladistic studies, such as those of Doyle & Donoghue (1986, 1992), so corroboration is currently precluded.

The general groupings of angiosperms (exclusive of *Ceratophyllum*) identified in these two analyses are highly similar to each other and to those of most recent taxonomic schemes, particularly those of Dahlgren (1980), Dahlgren et al. (1985), and Thorne (1992; this last has admittedly incorporated results of several molecular investigations). Furthermore, results of *rbc*S (Martin & Dowd, 1991) and ribosomal studies (Hamby & Zimmer, 1992) are quite similar to ours as well. How these larger groupings (clusters of families and in some cases orders) are inter-related is the point at which their similarity diverges. Although having quite different implications for angiosperm origins and evolution, the preferred hypothesis in one of these studies is not vastly different in relative parsimony from those favored in other investigations. For example, with mostly morphological data, Doyle & Donoghue (1986) discovered a "paleoherb rooting" at one step less parsimonious. Constraining a paleoherb rooting for angiosperms, at Nymphaeales (as in Hamby & Zimmer, 1992), was also only slightly less parsimonious in the subset of angiosperm *rbc*L sequences studied by Qiu et al. (1993, this issue). When examined to address basal angiosperm relationships, all these data appear to lack a strong historical signal.

A number of phenomena have been suggested to be capable of confounding molecular phylogenetic studies. We consider below several of these factors and examine their potential to affect studies of *rbc*L sequence variation and then address some additional concerns about future directions of molecular systematic study.

### EFFECTS OF PARALLEL NUCLEOTIDE SUBSTITUTIONS IN INDEPENDENT LINEAGES

An effect of unrecoverable (due to extinction) or unobserved (due to insufficient sampling) character-state changes is the introduction of spurious similarities, which may result in treatment of independently derived nucleotides at a given base position as homologous (see Albert & Mishler, 1992). Such mistaken interpretations of independent events can lead to "branch attractions" if an analysis includes a great number of such assessments (Felsenstein, 1978). Adequate taxon sampling, sometimes referred to as appropriate "taxon density," is one means of reducing potentially inaccurate assessments of similarity, but determining at what point sampling is sufficient has so far only been addressed in an a posteriori manner.

The improvement afforded to assessments of character-state change by increased taxon sampling is counterbalanced by a decrease in computational speed and ability to ascertain how near results are to maximum parsimony. Intrafamilial studies are not as likely to be affected severely by these problems because, in general, numbers of taxa are not as great and evenness of sampling is better. At higher taxonomic levels within seed plants, a paradoxical impediment to progress arises: if taxon number is great enough to assess character-

state changes accurately, then one reasonably can expect to reach only suboptimal phylogenetic solutions, but if taxon number is restricted enough to gain confidence of the maximum parsimony of the trees found, spurious assessments of character-state identity could obscure all but the closest relationships.

To evaluate relationships of Plumbaginaceae and Polygonaceae to families of Caryophyllales, Giannasi et al. (1992) used a number of phenetic and "phylogenetic" methods, including a Fitch-Margoliash dendrogram based upon genetic distances (Kimura, 1981; Felsenstein, 1990), maximum parsimony (PHYLIP, Felsenstein, 1990; PAUP, Swofford, 1991), and maximum likelihood (ML; Felsenstein, 1981). All three methods produced the same lack of resolution concerning relationships of these families; to state that Plumbaginaceae and Polygonaceae are "not closely related" (meaning "closely similar") to Caryophyllales does not preclude them nonetheless from being closest relatives. From the perspective of results presented here (Fig. 9A, B), spurious similarities in the data analyzed by Giannasi et al. (1992) appear to affect equally results of all three tree-building methods: *Gossypium* simultaneously attracts higher asterids and magnoliids (in our trees *Gossypium* is well imbedded among rosids; rosid II, Fig. 10A, B). (See Olmstead et al., 1992, 1993, this issue, for an example and discussion of the effects of taxon sampling.)

Prospects for improvements of tree-building methods with greater numbers of taxa exist (Penny et al., 1992). In the example of Giannasi et al. (1992), none of the methods employed succeeded in eliminating what we interpret as branch attractions due to the small number of taxa sampled and use of distantly related outgroups. Phylogenetic studies using morphological characters for a closely related group of rosid or asterid families would likely be affected adversely by outgroups of magnoliids or monocots. This phenomenon is perhaps even more probable with nucleotide data in which homology is initially assessed only by nucleotide position and character states are restricted to the same four alternatives. Character "homology" for distantly related taxa can be easily determined with *rbc*L data (i.e., a given nucleotide position in this size-conserved gene; "primary homology," de Pinna, 1991), but this does not mean that assessments of character-state homology (synapomorphy) are less subject to homoplasy than with other data.

If phylogenetic analyses of nucleotide data cannot be expected to reveal relationships when sampled with manageable numbers of taxa (from the standpoint of computation of minimal trees) and if sampling with sufficient numbers of taxa precludes assessing the parsimony of results, then we have reached an impasse until improved methods of analysis are developed. An appreciation of this problem has led us to be skeptical of the overall topologies presented (Figs. 1, 2), and competing ideas of relationships should not be overlooked when performing more restricted analyses of these and other gene sequences.

### INTERNAL SUPPORT FOR THE BROAD TOPOLOGY: AN AD HOC ANALYSIS OF SUBCLASS HAMAMELIDAE

For purposes of suggesting an appropriate manner to examine internal support of families traditionally recognized as a natural group, we selected one of the most controversial subclasses, Hamamelidae sensu Cronquist (1981), for which we have data from 18 of 24 families. Numerous phylogenetic and systematic studies of the Hamamelidae have been completed (see various authors in Crane & Blackmore, 1989). The morphological features suggesting a close relationship among these families are largely those associated with the temperate amentiferous syndrome, and these clearly could be the result of parallel modification in unrelated lineages. In their developmental characteristics and wood anatomy, families of Hamamelidae are particularly heterogeneous (Cronquist, 1981; Crane & Blackmore, 1989). In performing the broad analysis, we sought to avoid a priori ideas about what constituted monophyletic subgroupings of angiosperms, but for this heuristic example we have accepted ad hoc the outgroup relationships found in the general study.

We selected 72 species that included all members of Hamamelidae and their immediate sister taxa as identified in trees from both searches. No attempt was made to select species that would reproduce the particulars of the general topologies. A tree search under the Fitch (equal weights) criterion using 2,000 random sequence additions, MULPARS, STEEPEST DESCENT, and NNI branch-swapping (but permitting only 10 trees to be held at each step) found only one island at maximum parsimony (i.e., all trees could be found by single branch swaps using any one of them as a starting tree; cf. Maddison, 1991). Additional as well as shorter islands could still exist but are unlikely after 2,000 repetitions (this type of search required about 24 hours to complete on a Macintosh Quadra 950 with 20 MB of RAM). After random addition searches were completed, the trees

found were used as starting points in a single analysis with MULPARS on and TBR swapping to completion; this process should find all equally parsimonious trees in the single island identified. Our search found 36 equally parsimonious Fitch trees, three of which were optimal under the weighting criterion of Albert et al. (1993, this issue; see Materials and Methods). One of these was randomly selected and is shown with Fitch branch lengths (ACCTRAN optimization; Fig. 16). The tree length was 2,234 steps, the C. I. was 0.288 (excluding unique characters), and the R. I. was 0.532. The maximum parsimony trees also were used to search for trees up to five steps less parsimonious under the Fitch criterion; the FILTER TREES option was used to identify trees at each length, and a strict consensus tree at each step was computed. The number of steps less parsimonious at which each topological component decayed was recorded (Fig. 16; "decay values" are shown below the branches: "d0" indicates that the branch is a polytomy in the strict consensus of the maximum parsimony trees, "d1" indicates that the branch is a polytomy in the consensus tree at one step less parsimonious, etc.).

This analysis identified eight lineages into which members of Hamamelidae fell (Fig. 16): *Eucommia*, clade A, sister to *Aucuba* (Cornaceae) and *Garrya* (Garryaceae) and nested within an asterid clade; Hamamelidaceae, Cercidiphyllaceae, etc., clade B, in a series paraphyletic to Saxifragaceae–Grossulariaceae; Fagales, etc., clade C, sister to Fabaceae–Polygalaceae; Urticales, clade D, sister to Rosaceae; *Leitneria*, clade E, nested within families of Sapindales; isolated Trochodendrales, clade F, sister to Buxaceae; *Platanus*, clade G, situated in a heterogeneous group; and the last, *Euptelea*, clade H, situated among Ranunculales. Many of these clades are well supported internally, decaying at three or more steps less parsimonious (some, such as Trochodendrales Buxaceae and the *Platanus* assemblage are weakly supported as monophyletic lineages but clearly are not members of other well supported groups, leaving them in isolated positions apart from other Hamamelidae).

Results of this restricted analysis are congruent with the topology found in the broad searches (Figs. 1, 2) and indicate the level of internal support demonstrated by *rbc*L data. Future studies could combine morphological data with this molecular matrix and perform constraint experiments in which various rearrangements of these taxa are examined for their relative degrees of parsimony. The general conclusion from this example is that the Hamamelidae do not form a monophyletic lineage; they are shown to be grossly polyphyletic. Besides the amentiferous syndrome, the major trait of Hamamelidae is the presence of tannins, which is likewise compatible with a relationship to the other tannin-containing families, Fabaceae, Rosaceae, Saxifragaceae sensu stricto, and Crassulaceae. Many authors (e.g., in Crane & Blackmore, 1989) have discussed these families in terms of which are "lower" and which are "higher" families. This distinction finds some support from these results; the "lower" groups either stand in an isolated position near the base of the eudicots (Eupteleaceae, Platanaceae, and Tetracentraceae–Trochodendraceae) or basal within rosids (rosid IV, Fig. 2A; Daphniphyllaceae, Hamamelidaceae, and Cercidiphyllaceae), whereas most "higher" hamamelids (Casuarinaceae, Fagaceae, Moracae, Ulmaceae, and Urticaceae) demonstrate a well supported relationship to Fabaceae or Rosaceae ($d > 5$ on two branches at the base of the largest clade in Fig. 16). The position of *Leitneria* in Sapindales near Burseraceae is corroborated by a shared suite of secondary compounds and presence of intercellular resin canals.

The example presented above is not intended to be more than a superficial phylogenetic treatment of families traditionally referred to Hamamelidae. It is meant to serve as an example of how the general topology, which itself is suspected of being suboptimal and presently cannot be examined by decay analysis because of its size, may identify a relevant analysis within which questions of optimality and relative support can be addressed. We are pleased that general relationships found in the broad analyses hold up well when addressed in this and other more restricted investigations, none of which have found vastly different topologies.

### ON THE INFORMATIVENESS OF ALL SUBSTITUTIONS

The majority of character-state changes in protein-coding genes have been demonstrated to occur at third positions within codons, and numerous empirical studies have shown third position substitutions to be more abundant in this and other data sets. Some workers have experimented with discarding third position substitutions from their analyses or analyzing nucleotide sequences inferred from amino acid data (which standardizes all synonymous substitutions; Martin & Dowd, 1991). In several studies (Conti et al., 1993, this issue; Donoghue et al., 1992; Kim et al., 1992; Smith et al., 1993, this issue), all three codon positions have been found to exhibit similar levels of homoplasy (and perhaps similar rates of change per site as

well). It has generally been assumed that, for most genes at some unspecified higher taxonomic level, third positions become saturated and therefore are more likely to be uninformative or even misleading (Swofford & Olsen, 1990), hence the "logic" for discarding third positions and using only nonsynonymous substitutions. In the empirical studies cited above, multiple substitutions apparently have occurred at certain first and second positions at low taxonomic levels (i.e., within families). Variable third positions appear as consistent on average as variable first or second positions, thus making them as reliable at reconstructing relationships (as a class perhaps they are better because they are more numerous; Donoghue et al., 1992).

Whether factors such as codon usage (tRNA biases known to favor only a subset of the possible third position nucleotides for a given amino acid) might contribute to the relatively higher consistencies of some synonymous substitutions is a topic that should be investigated. Codon usage is usually studied in a pairwise fashion, but it would be better examined from a phylogenetic perspective. Most molecular models, including the one (a modified version of that of Kimura, 1980) that is the basis for the weighting scheme used here (Albert et al., 1993), are arguably too simplistic in their assumptions concerning patterns of nucleotide substitutions. Ultimately, we could imagine that knowledge of processes, specific to *rbc*L, responsible for the higher consistencies of some synonymous substitutions might permit construction of alternative weighting models that would extract more historical signal from *rbc*L (Albert et al., 1992a). Until we better understand evolutionary constraints on all positions within a coding sequence, it seems most prudent to use methods that do not eliminate any evidence of the underlying process.

### BRANCH LENGTH INEQUALITIES AND UNEQUAL RATES

The fossil record suggests an early, and perhaps rapid, diversification of angiosperms (e.g., Doyle & Hickey, 1976). Several different categories of specialized flowers appeared nearly simultaneously in geological terms. These included strobiloid types characteristic of Magnoliales, simpler forms similar to those of Laurales, highly reduced sorts like those of Piperaceae and Chloranthaceae, and catkin-bearing specimens comparable to those of lower hamamelids (i.e., eudicots like Platanaceae; Schwarzwalder & Dilcher, 1991). Most of the segments are short in the basal portion of the *rbc*L trees (but not the branches of monocots or eudicots; Fig. 2A, B), which could be interpreted as support for hypotheses that production of diverse flower types took place rapidly and early in angiosperm evolution.

Nonetheless, other explanations could explain patterns of uneven distribution of character-state changes identified by this and many other analyses of molecular data (e.g., Jansen & Palmer, 1988). These include episodic changes of rates of sequence divergence and effects resulting from an uneven distribution of sampled taxa that could cause certain character-state changes to be assigned to several more terminal branches rather than to a single, more internal one. The latter effect could be explained if subsequent substitutions over the long history of groups obscured or even eliminated evidence of synapomorphic character states for these groups. Greater sampling of variation within terminal groups may result in character states being optimized to a single, more basal branch, with reversals and further changes in terminal lineages, as opposed to being optimized to appear as independently arising in several terminal groups. Several other factors, including the specific method of optimization and interpretation of the robustness of groups with "weak" character-state support, are considerations relevant to the distribution of homoplasy. This is another area in which future emphasis should be placed because advances (supported by theoretical considerations) in understanding the effects of character-state optimization could improve evaluation of critical innermost branches.

Lineage-specific rate asymmetry, a potential contributor to spurious branch attractions (Hendy & Penny, 1989; Albert et al., 1993, this issue), is significant for *rbc*L (Bousquet et al., 1992), yet may not be extensive enough between lineages to be problematic. Initial estimates of total sequence divergence rate per year produced a range of $5–7 \times 10^{-10}$ for (i) panicoid versus pooid grasses (Doebley et al., 1990), (ii) *Petunia* versus *Tobacco*, and (iii) *Colchicum* versus *Lilium* (Wendel & Albert, 1992, from data presented in Albert et al., 1992a). Subsequent studies of woody magnoliid taxa with austral disjunction patterns (and for which plate tectonics suggest appropriate divergence times) have indicated divergence rates ranging between $4–5 \times 10^{-11}$ and $1.4–1.7 \times 10^{-10}$ (V. A. Albert, unpublished; note that all rates presented are for lineage pairs, and so the average rate for each lineage is half the figure shown). Only the lowest of these rates is approximately an order of magnitude different from the herbaceous taxon comparisons. Wilson et al. (1990) indicated slightly slower rates for palms. Recent work on monocots

using relative rate tests (Gaut et al., 1992) demonstrated five-fold variation for *rbc*L, which still falls within the range cited above. Although 5–10-fold differences in rates would appear potentially to contribute enormous branch-length differences, the small overall rates involved mean that great divergence times would be a more important factor. In addition, differences in rates appear to be highly lineage-correlated (for example, in graminoids; Gaut et al., 1992) rather than random, and if more extensive sampling at lower taxonomic levels is possible in these "fast" clades, then effects of rate differences can be offset.

Most if not all *rbc*L rates will probably exist within a relatively narrow "window," perhaps approximating the range illustrated above ($10^{-10}$–$10^{-11}$, V. A. Albert, M. W. Chase & J. F. Wendel, unpublished). If that is correct, lineage-specific rate inequalities are unlikely to be a primary factor in branch attraction; rather, asymmetrical divergence times would be implicated because the product of rate and time is the central parameter in considerations of potential systematic errors (see Albert et al., 1993, this issue). Thus uneven sampling or extinction of lineages may present greater problems than do differences in rates.

### EFFECTS OF LATERAL GENOME TRANSFER, ANCESTRAL POLYMORPHISMS, AND DIFFERENT MODES OF INHERITANCE

The trees presented here represent only information from a single gene, and factors peculiar to its evolution could lead to erroneous results. Several of these phenomena are discussed below, but we feel that their impact is likely minimal. Genome transfers would result in all or parts of a genome being phylogenetically coherent (transferred as a unit) at the time transit occurs (Doyle, 1992; Rieseberg & Soltis, 1991), but before and after movement most characters within genomes evolve independently (although still linked if on the same chromosome) and ought to be expected to contain historical evidence. Hybridization is unlikely to influence phylogenetic analyses except at lower taxonomic levels. Even matings between divergent parents still occur within portions of families (and usually among closely related species in a genus) rather than between families. Parental taxa at the time of an ancient hybridization also were likely closely related, and in these genomes highly conserved loci, such as *rbc*L, would have been similar or even identical.

Ancestral polymorphisms (Pamilo & Nei, 1988; Wu, 1991; Doyle, 1992) also affect only closely related taxa, and, like the effects of ancient hybridization, those of ancient polymorphisms would likely be minor relative to subsequent genetic divergence. If lineages that contain polymorphisms diverged in a closely spaced manner and uneven sorting did take place, it is unlikely that any evidence of such variation within a progenitor could be identified as such over the great amounts of time involved in this study. Furthermore, polymorphisms are short-lived and are undocumented for conservative, single-copy loci, such as *rbc*L. At most these effects would be highly localized among groups of closely related terminal taxa and, with adequate taxon sampling, would not be expected to perturb greatly the results.

Lateral transfers not involving exchange of gametes (by unknown mechanisms) may have occurred between major lineages in the past (i.e., of *rbc*L from a purple bacterium to a red algal ancestor; Morden et al., 1992). Such transfers presently appear rare among land plants and seed plants in particular; furthermore, artificial transformations are relatively difficult and often have a destabilizing or transient effect on transformed plants. While we must admit that this is an unknown area that could have played a role in certain anomalous placements in the *rbc*L trees (e.g., *Montinia* and *Vahlia* of Saxifragaceae sensu lato among asterids; Fig. 15), at the same time we are not prepared to advocate it as a scenario until trees based on other data demonstrate a pattern consistent with such hypotheses (as in the example of Morden et al., 1992). Using evidence from studies of secondary chemistry and development, Morgan & Soltis (1993, this issue) build strong cases for the highly dispersed groupings found in their study of Saxifragaceae sensu lato. Furthermore, many of their findings were also congruent with recent investigations of non-molecular characters. Rather than resorting to explanations involving lateral transfers of chloroplasts by mechanisms about which we can only speculate, we would prefer first to examine specific cases from a cladistic perspective rather than from that of current taxonomic schemes.

An *rbc*L tree is not solely a maternal tree. Although chloroplast transmission is principally maternal and uniparental, several groups exhibit a paternal (e.g., conifers) or biparental pattern (Neale et al., 1986; Szmidt et al., 1987; Whatley, 1982; Wagner et al., 1987; Corriveau & Coleman, 1988; White, 1990; Owens & Morris, 1991). Others that have been thought most probably maternal, such as *Liriodendron* and *Magnolia* (Corriveau & Coleman, 1988), consistently exhibit 5–15% paternal inheritance (Sewell et al., 1993). The potential

effects of a mixed pattern of inheritance on gene trees are also unlikely to affect studies at interfamilial levels and above.

## GENES VERSUS TAXA

One of the more persistent controversies surrounding molecular phylogenetic studies has centered on whether results, at a given taxonomic level, will be "improved" more by adding additional taxa sequenced for the same gene or by adding sequence analyses of additional genes for the same set of taxa (analyzed simultaneously or each performed independently for assessments of congruence; Pamilo & Nei, 1988; Wu, 1991). From the standpoint of corroboration, phylogenetic studies of other data sets are absolutely crucial. Nevertheless, it seems quite clear from our work on these data sets that ideas of relationships have changed considerably as more taxa have been added. We suspect that no single gene sequence can provide reasonable hypotheses of relationships of seed plants when sampled uncritically and superficially, but perhaps erroneous results from one locus would be "corrected" by stronger signals present in the others. Data to evaluate this most critical question do not exist: would separately analyzing 20 gene sequences for the same set of 25 to 30 taxa produce well supported relationships?

We are convinced that adding representatives of the still numerous and diverse families absent from this analysis has the potential to enhance assessments of relationships at all levels (despite obvious computational complications). A great deal of the variation present within the gene still remains to be sampled taxonomically. Studies in several groups of plants indicate that *rbc*L often can be valuable at rather low taxonomic levels (Albert, in press, in the slipper orchids; S. Graham, B. Morton & S. Barrett, unpublished, in *Eichhornia*; R. Price & J. Palmer, unpublished, in *Pelargonium*; S. Williams & M. Chase, submitted, in *Drosera*; Xiang et al., 1993, this issue, in *Cornus*). What can be concluded from these studies is that although it is absolutely critical that more genes be studied to provide corroboration, it is unlikely that any of these studies will make a contribution to understanding seed-plant relationships if the level of sampling is too sparse. Only empirical studies will ultimately resolve the "genes versus taxa" controversy. We estimate that by the time this paper is in print, more than 1,200 sequences of *rbc*L from seed plants will exist, and future studies will undoubtedly benefit from this enormous database.

An additional implication of adding more taxa is that the results presented here may not be stable or reflective of those of an analysis of two, three, or four times as many sequences. We point to two regions of the general topology that are morphologically quite heterogeneous and that we believe are possibly generated by undersampling: hamamelid II (Figs. 2A, B, 7A, B) and rosid I (Figs. 2A, B, 11A, B, C). In the former, the critical taxa needed to provide more appropriate relationships could be some of the still-unsampled families, but these groups (represented by *Lambertia*, *Nelumbo*, *Platanus*, and *Sabia*) could just as likely represent the isolated relicts of now largely extinct lineages. In the case of rosid I, only a small percentage of the families has been sampled (for instance, only 7 of 24 families in the Violales: Dilleniidae), and it is in such a case that we might predict "curious" sister-group relationships. Topological instability often occurs in cases where long terminal branches are next to short internal branches, that is, hypothesized relationships are drastically altered by the addition of related taxa that "break up" long branches. Two surprising pairs of sister taxa from Search I, *Erythroxylum–Viola* and *Ochna–Drypetes*, are quite divergent and connected to each other by relatively short branches (Fig. 11A; branch lengths shown only in 11B). In Search II, the addition of *Reinwardtia* displaced *Erythroxylum* from *Viola* to *Drypetes*, leaving *Ochna* to stand isolated from any other taxon (Fig. 11B). In such situations, assessments of relationships are difficult, but, as more closely related species are added, distinguishing synapomorphies for families and groups of families as distinct from autapomorphies for individual species will become more reliable. We would not argue that the relationships found for rosid I are "better" in Search I than in Search II (or vice versa), but rather point these out as areas of the trees that require additional sampling and in which many of the relationships suggested by these analyses of *rbc*L have little or no morphological support.

## VALUE OF THE BROAD ANALYSIS

We view the relatively robust internal support found by evaluations of portions of the broad analysis as an indication that *rbc*L sequences contain information relevant to the evolutionary history of angiosperms (Fig. 16, on Hamamelidae and most of the other papers in this issue; in particular see Conti et al., 1993, and Rodman et al., 1993, for which comparable cladistic analyses of non-molecular data are also available and compared). Well-

characterized families and groups of families (as evidenced in several more restricted studies of morphology, anatomy, and secondary chemistry; e.g., Rodman, 1991a, b; Hufford, 1992) are largely congruent with our results. Other evidence supports the monophyly of the angiosperms (Doyle & Donoghue, 1986, 1992), monocots (Dahlgren et al., 1985), and eudicots (Donoghue & Doyle, 1989). Likewise, the position of *Ceratophyllum* as sister to the rest of the angiosperms compares favorably with the fossil record (Les, 1988; fossil fruits from 120 million years ago are identical to extant fruits, D. Dilcher, pers. comm.). The status of the families of the Papaverales–Ranunculales collectively as sister to the rest of the eudicots (Figs. 1, 2) also finds ample external support (Donoghue & Doyle, 1989, among others).

The results reported here do find some "surprising" relationships. Several families, such as Chenopodiaceae (Fig. 9A, B) and Berberidaceae with only two representatives each in our studies, are paraphyletic to other families. These results do not surprise us because sampling has been demonstrated repeatedly to be a major factor, and insufficient or uneven sampling can generate anomalous relationships. Concomitantly, our results emphasize the need for studies of familial limits to include much better taxon sampling than is generally the case in these two analyses. Some of these instances of paraphyly may be accurate; many pairs of temperate, herbaceous/woody, tropical families have long been suspected of being unnatural (for example, Lamiaceae are derived within Verbenaceae and Brassicaceae within Capparaceae in our studies).

Other "major" findings of this study, although discordant when viewed from the perspective of various taxonomic treatments, find support from recent studies of non-molecular characters. For example, the placement of Ericales as sister to asterids (Figs. 1, 2) was also found by Hufford (1992), and the monophyly of most mustard-oil families (Fig. 10A, B) was previously suggested by Rodman (1991b). Other sets of relationships are unique to this analysis and require more thorough morphological and molecular studies. These include: (i) the position of several families with polypetalous corollas and supposed affinities to Saxifragaceae among each major lineage of Asteridae (requiring a hypothesized reversal of the sympetalous condition in *Escallonia*, *Montinia*, *Phyllonoma*, and *Vahlia* (all Saxifragaceae sensu lato); (ii) nesting of dilleniid orders Capparales, Malvales, Theales, and Violales among rosid clades (the systems of both Dahlgren, 1980, and Thorne, 1992, treated these groups in a manner somewhat similar to our topology); (iii) relationships of Nepenthaceae and Droseraceae to Caryophyllidae sensu lato (Fig. 9A, B); and (iv) specific associations of numerous problematic genera like *Dillenia* (among rosids near Caryophyllidae, Fig. 9A, or near the base of the asterids, Fig. 12B; see Olmstead et al., 1993, this issue), *Impatiens* (near members of Ebenales and Ericales; Fig. 13A, B), and *Nelumbo* and *Lambertia* (among lower hamamelids; Fig. 7A, B). Placement of most of these genera and families has varied substantially among recently proposed classifications (although no one has suggested the relationships found here), and their positions in this study will undoubtedly add to the controversies.

Because additional lineages were present in Search II and different methods were used to construct the trees, it is impossible to evaluate whether the topology found in Search II represents a different island of trees. Indeed, multiple islands of equally parsimonious trees were found in other studies in this issue: Morgan & Soltis (1993), Olmstead et al. (1993), and Qiu et al. (1993). Certainly shifts of some taxa, especially *Paeonia* from a basal asterid to sister of Crassulaceae and Saxifragaceae sensu stricto, suggest a radically different explanation of the distribution of at least some characters. *Paeonia* is well supported internally in its new position (its sister status to *Ribes* does not decay even at five steps less parsimonious; Fig. 16). Shifts of *Dillenia*, *Gunnera*, Santalales, and *Vitis* seem, at first glance, to be major alterations of position, but branches are so short near the split between asterids and rosids that these could not involve many additional steps in either topology (Fig. 2B).

Although the trees of Search II are preferred to those of Search I because some of them were swapped on to completion and therefore are more likely to represent at least a local optimum, taxonomic conclusions based on either search are untimely. When faced with the fact that large numbers of angiosperm families are still unrepresented in the *rbc*L data set, we would argue that a valid assessment of the most appropriate positions of many taxa, such as *Dillenia*, *Gunnera*, and *Vitis*, grossly premature. Some conclusions, polyphyly of Hamamelidae and Dilleniidae, for example, seem well supported now.

This study is noteworthy not only for its scope but also for the large number of contributors whose unpublished sequences made up the bulk of the data analyzed. This wide collaboration was advantageous to all workers; many found that taxa sequenced by other laboratories supposedly working

on distantly related groups (in recent taxonomic schemes) fell into or near their group of interest. Prime examples of this are the close phylogenetic relationship of Nepenthaceae and Droseraceae to families of Caryophyllidae, Pittosporaceae to Apiaceae–Araliaceae, Malvales and Capparales (both "dilleniids") to Sapindales, and *Corokia* (Cornaceae) to Asteraceae.

Broad analyses are thus important in providing evaluations of a priori assumptions about appropriate sets of study taxa for more focused and rigorous studies; they should be formalized so that someone takes the initiative to perform them. Governmental funding agencies should facilitate studies, such as the one presented here, that are well beyond the scope of individual laboratories. This study demonstrates the potential of this kind of analysis, but no single individual or laboratory could have received formal support for sampling this diverse set of taxa and performing the phylogenetic analysis; it would have been deemed by reviewers too broad and too unfocused. Although extramural funds supported most of the other studies in this issue, no support was received specifically for the broad analysis. It is the investment in individual studies that justifies a further expenditure to support syntheses that supply an essential overall perspective, even though they may be necessarily approximate.

The benefits of performing this largest-yet phylogenetic study of seed plants lie not only in support of specific relationships hypothesized by other studies (e.g., the sister group status of the Ericales and higher asterids proposed by Hufford, 1992) and in identification of previously unhypothesized monophyletic groups. This study also presents a comprehensive, explicit hypothesis for higher level relationships, permitting and encouraging initiation of studies evaluating other character systems that may show congruence with the major lineages of seed plants described here. We have performed none of the essential experiments that these results suggest (topological constraints, removal of characters, combining morphological with molecular data, etc.) and have not developed implications these topologies may have for specific character transformations in seed plants or molecular evolution of *rbc*L or RuBisCO. Believing that serious consideration of the significance of these general topologies is best handled at the more manifest level of other papers published here (and elsewhere), we have chosen instead to emphasize reasons for caution. We are content to present the findings of these studies as examples of potential benefits and pitfalls of such exercises. At the least, these analyses represent an attempt to improve both our understanding of seed-plant evolution and methods of phylogenetic inference. Corroboration by other data sets analyzed in a similar fashion is by far the most significant measure of relationships proposed here, and we hope this process of evaluation will be innervated by our efforts.

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[8] Department of Biology, Indiana University, Bloomington, Indiana 47405, U.S.A. Current address for RAP: Department of Botany, University of Georgia, Athens, Georgia 30602, U.S.A.

[9] Department of Biology, Texas A & M University, College Station, Texas 77843, U.S.A. Current Address for JHR: Department of Biology, College of the Ozarks, Point Lookout, Missouri 65726, U.S.A.

[10] Department of Botany, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.

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[13] Department of Botany, Arizona State University, Tempe, Arizona 85287, U.S.A.

[14] Institutionen För Systematisk Botanik, Uppsala Universitet, Uppsala S-751 21, Sweden.

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[19] Department of Biology, Lebanon Valley College, Annville, Pennsylvania 17003-0501, U.S.A.

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[21] Department of Biological Sciences, Wayne State University, Detroit, Michigan 48202, U.S.A.

[22] Department of Botany, University of Toronto, Toronto, Ontario M5S 3B2, Canada.

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**1A**

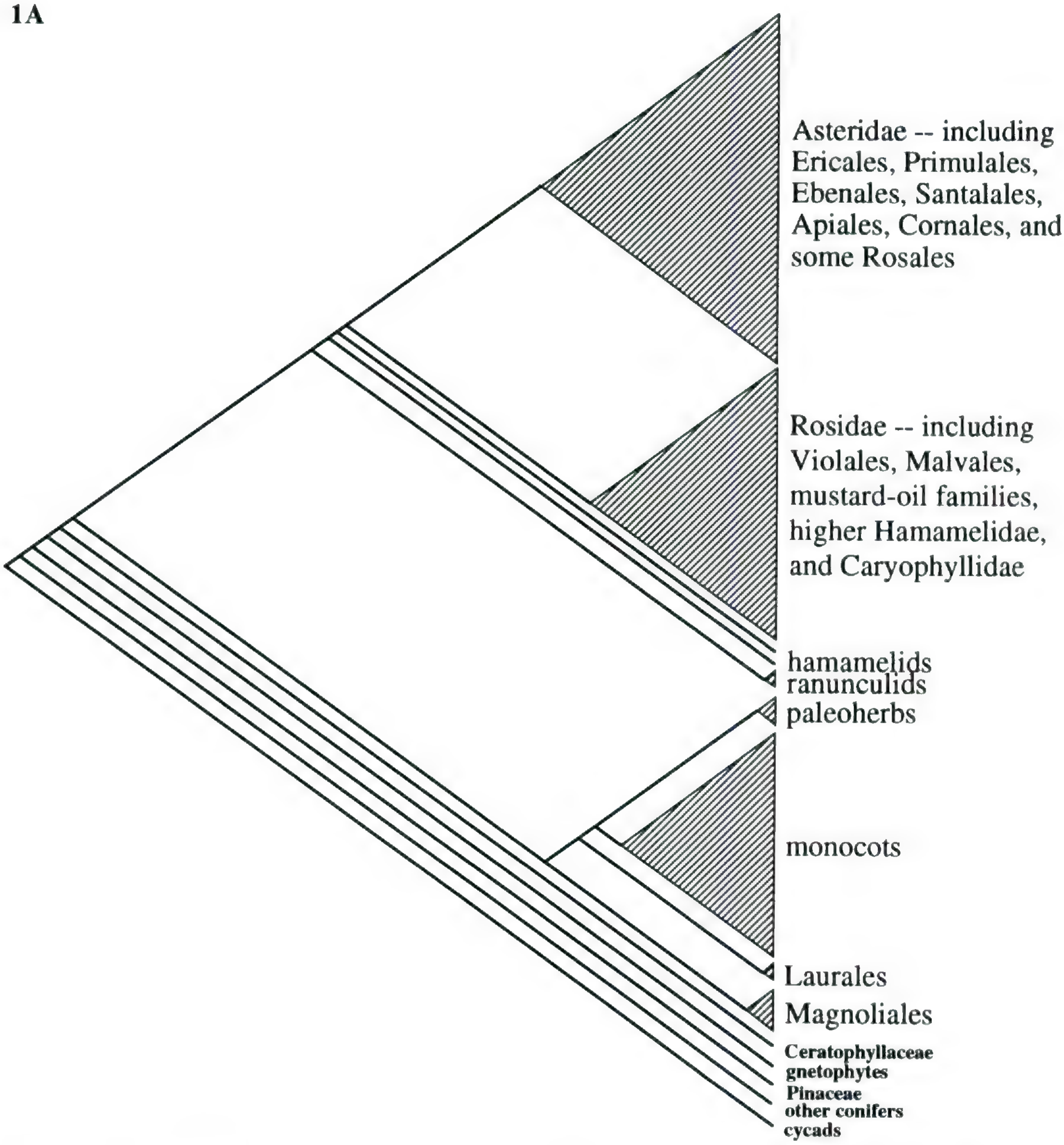
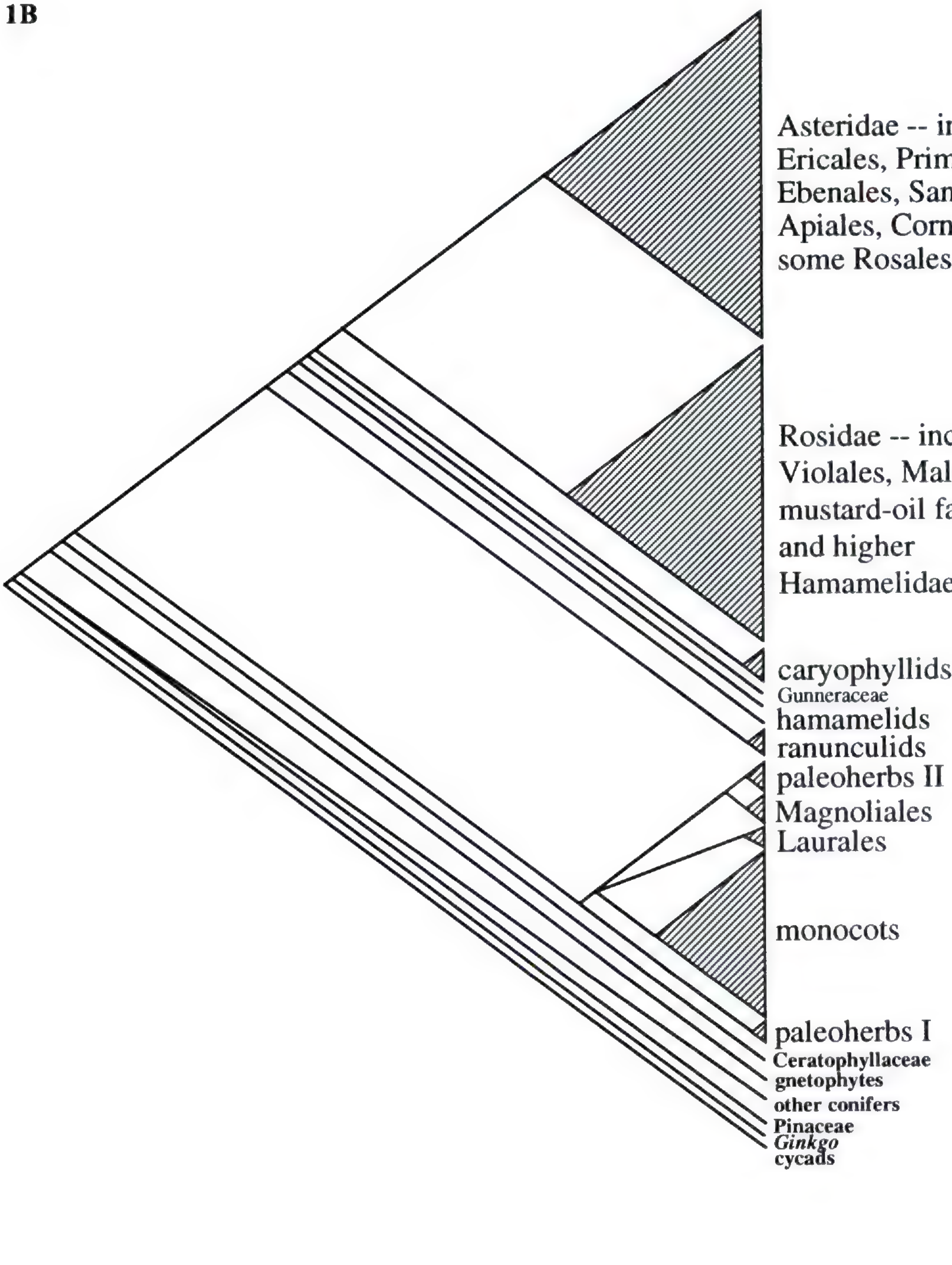



FIGURE 1. Summaries of the major clades identified in: (A) the combinable component consensus tree of 500 equally parsimonious trees found for 475 taxa using the character-state weighting method of Albert et al. (1993, this issue); and (B) the strict consensus tree of 3,900 equally parsimonious trees for 499 taxa found using the Fitch (even weights) criterion. These are ingroup networks arranged arbitrarily with the cycads sister to all other seed plants.

**1B**


Asteridae -- including Ericales, Primulales, Ebenales, Santalales, Apiales, Cornales, and some Rosales
Rosidae -- including Violales, Malvales, mustard-oil families, and higher Hamamelidae
caryophyllids
Gunneraceae
hamamelids
ranunculids
paleoherbs II
Magnoliales
Laurales
monocots
paleoherbs I
Ceratophyllaceae
gnetophytes
other conifers
Pinaceae
Ginkgo
cycads

2A

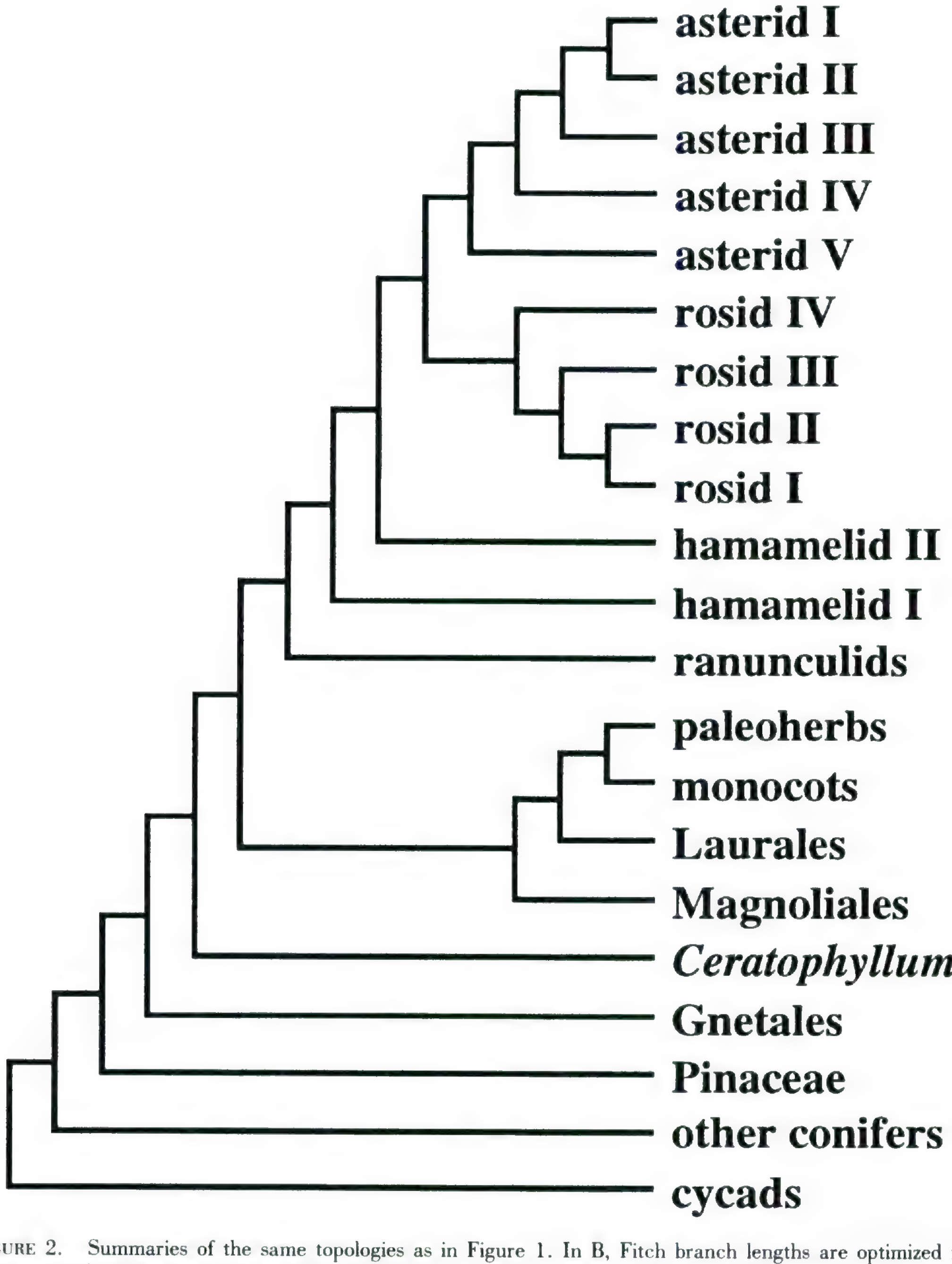
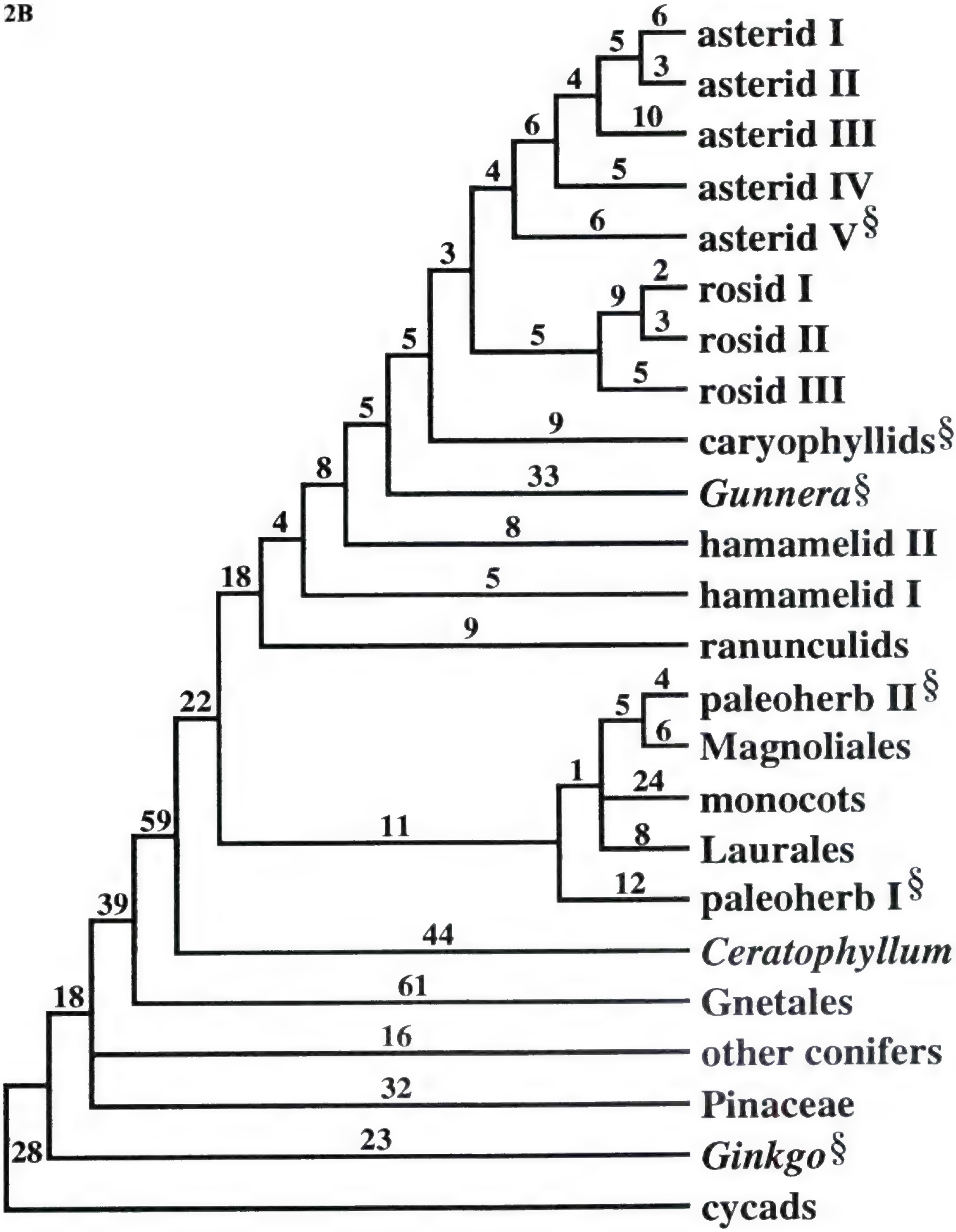



FIGURE 2. Summaries of the same topologies as in Figure 1. In B, Fitch branch lengths are optimized from a single tree; optimization on consensus trees is likely to overestimate branch lengths. Names of the specific clades identified do not conform to the composition of families used in most taxonomic schemes, but rather are designated with respect to the components of the major lineages (i.e., by the subclass name for the majority of taxa included, except for the heterogeneous hamamelid I, which is so designated because of its position and inclusion of Platanaceae). Names of each clade correspond to groups shown in Figures 3–15. Clades marked with a "§" in B are those that differ significantly in position or composition from A.

**2B**


6
5
3
4
10
6
5
4
6
3
2
9
3
5
5
5
9
5
9
8
33
4
8
18
5
9
22
4
5
6
1
24
59
11
8
39
12
44
18
61
16
32
28
23
asterid I
asterid II
asterid III
asterid IV
asterid V§
rosid I
rosid II
rosid III
caryophyllids§
Gunnera§
hamamelid II
hamamelid I
ranunculids
paleoherb II§
Magnoliales
monocots
Laurales
paleoherb I§
Ceratophyllum
Gnetales
other conifers
Pinaceae
Ginkgo§
cycads

3A

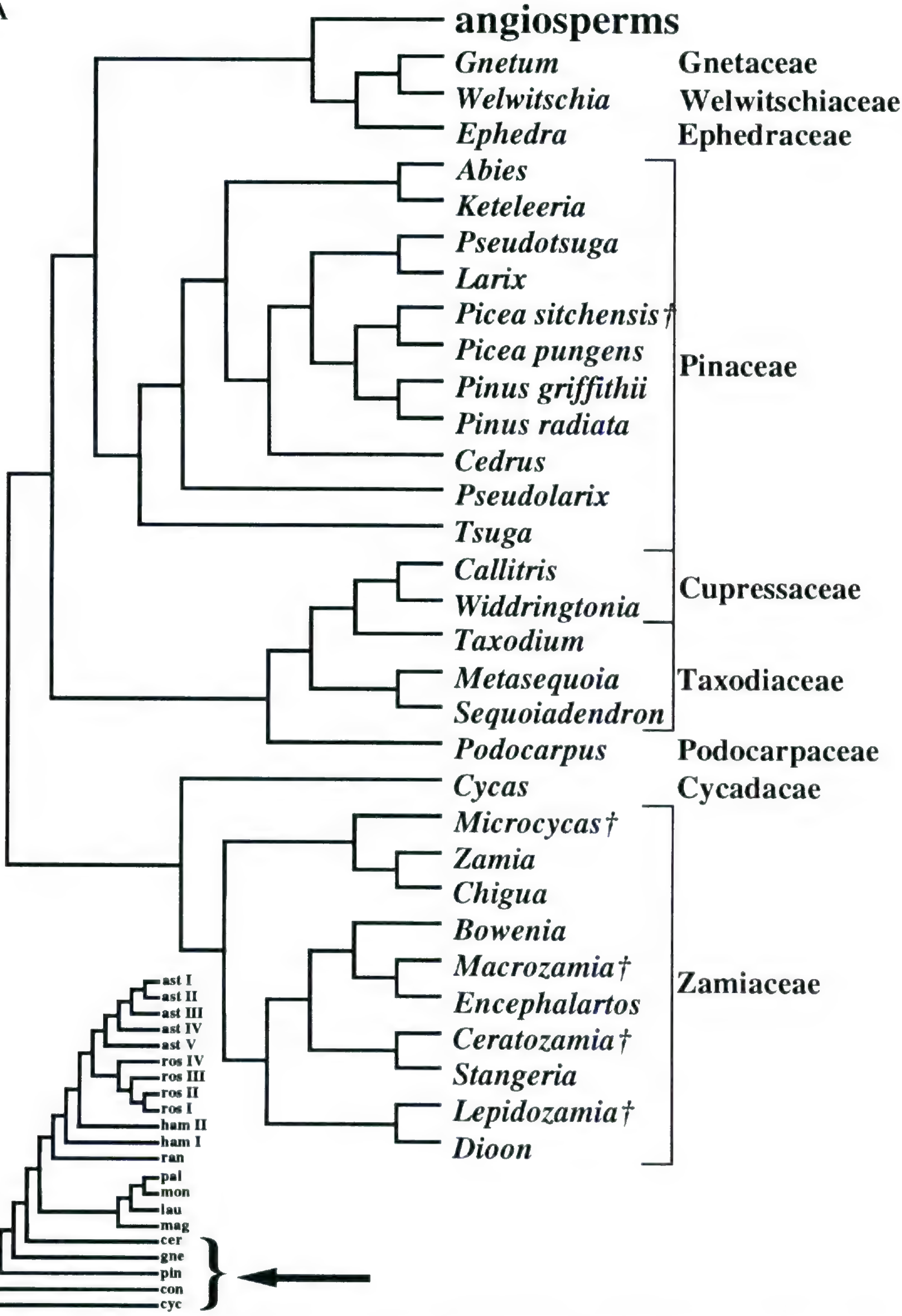
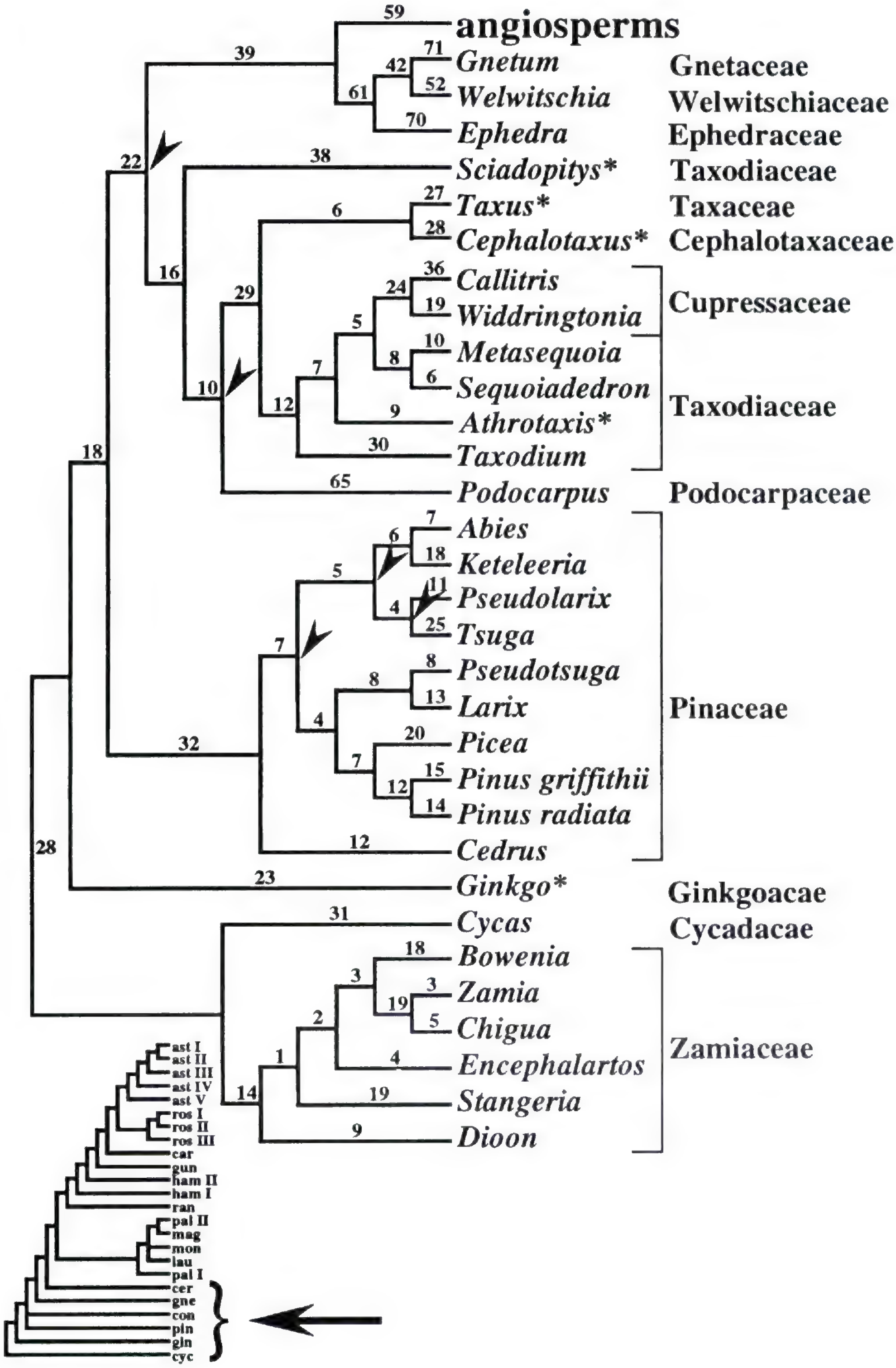



FIGURE 3. A portion of the overall analysis showing the "gymnosperms." (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow. Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B were not available for Search I.

**3B**


59
angiosperms
39
71
Gnetum
Gnetaceae
42
52
Welwitschia
Welwitschiaceae
61
70
Ephedra
Ephedraceae
22
38
Sciadopitys*
Taxodiaceae
27
Taxus*
Taxaceae
6
28
Cephalotaxus*
Cephalotaxaceae
16
36
Callitris
24
19
Widdringtonia
Cupressaceae
29
5
10
Metasequoia
8
7
6
Sequoiadedron
10
12
9
Athrotaxis*
Taxodiaceae
18
30
Taxodium
65
Podocarpus
Podocarpaceae
7
Abies
6
18
Keteleeria
5
11
Pseudolarix
4
25
Tsuga
7
8
Pseudotsuga
8
13
Larix
4
20
Picea
32
7
15
Pinus griffithii
12
14
Pinus radiata
Pinaceae
12
Cedrus
28
23
Ginkgo*
Ginkgoacae
31
Cycas
Cycadacae
18
Bowenia
3
3
Zamia
19
5
Chigua
2
1
4
Encephalartos
14
19
Stangeria
9
Dioon
Zamiaceae
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc

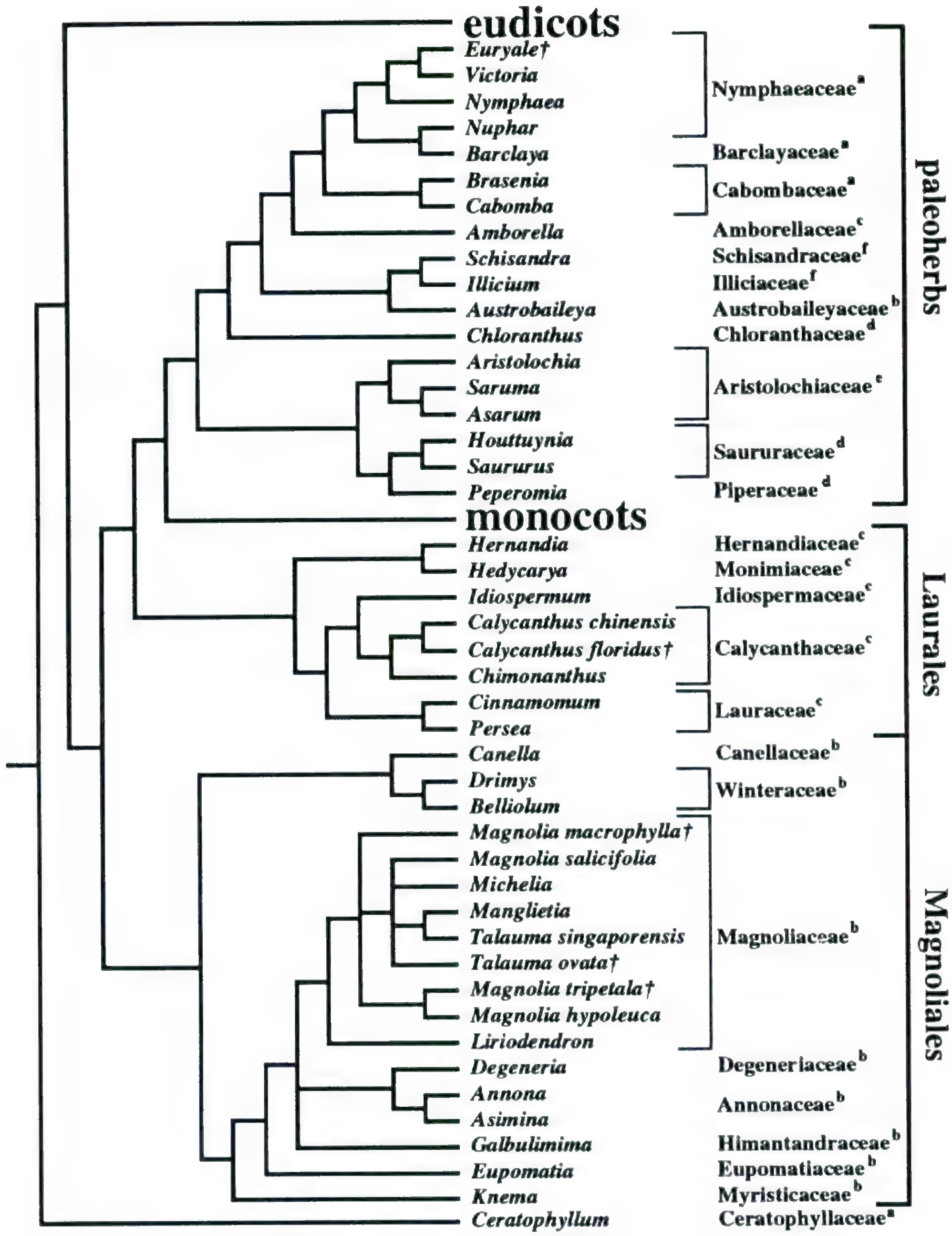
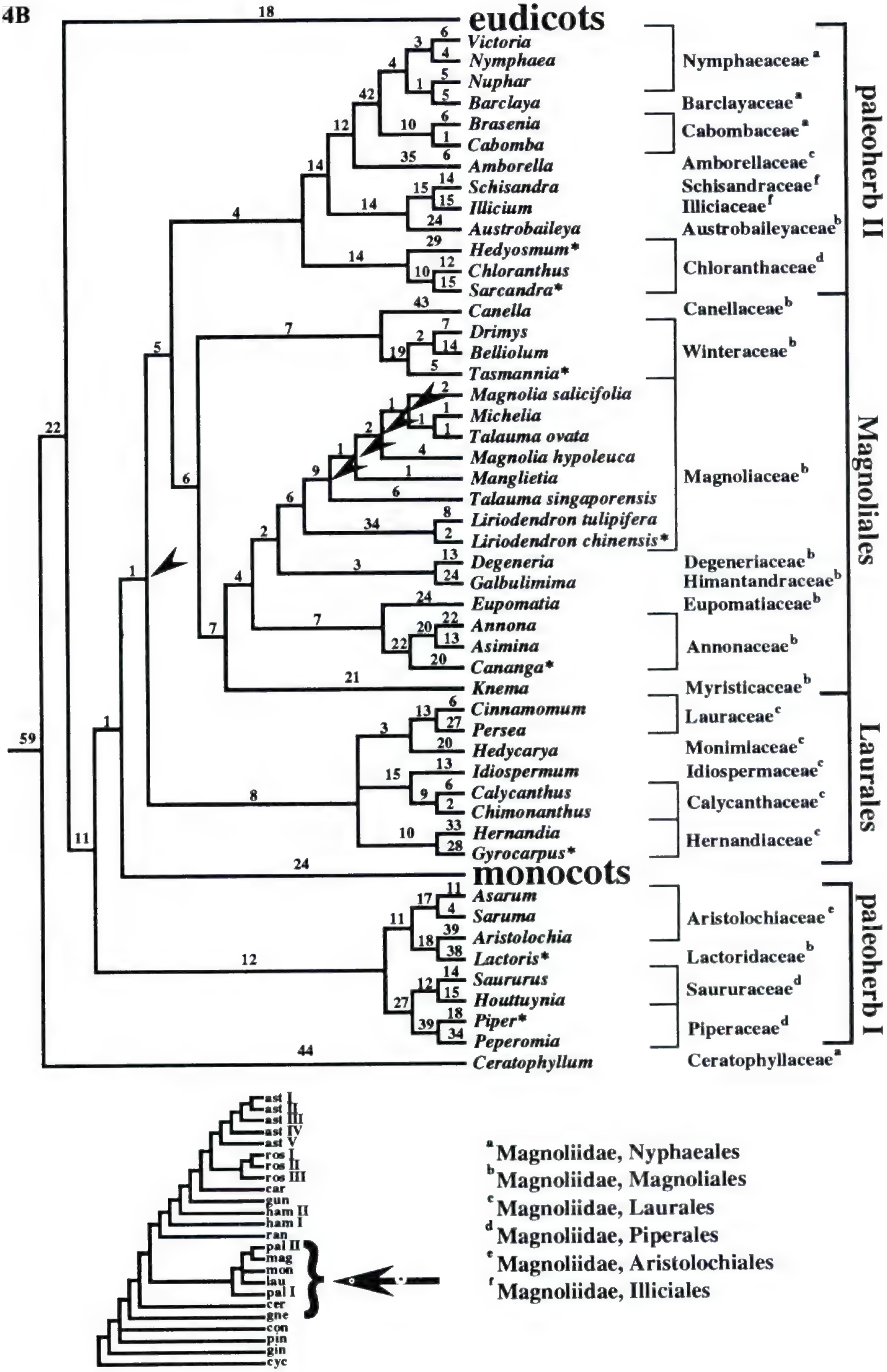



FIGURE 4. Basal portion of the overall analysis showing the positions of Ceratophyllaceae (inaperturate pollen), monocots (uniaperturate pollen), eudicots (dicots with triaperturate pollen), and the three clades of "primitive" dicots (monosulcate pollen). Note that, exclusive of *Ceratophyllum*, the angiosperms form two sister groups marked by the general pollen aperture number (one versus three). (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B were not available for Search I. The "*Canella*" in this figure represents the position of two sequences amplified from a total cellular DNA template (see Materials & Methods). Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

**4B**


eudicots
Victoria
Nymphaea
Nuphar
Barclaya
Brasenia
Cabomba
Amborella
Schisandra
Illicium
Austrobaileya
Hedyosmum*
Chloranthus
Sarcandra*
Canella
Drimys
Belliolum
Tasmannia*
Magnolia salicifolia
Michelia
Talauma ovata
Magnolia hypoleuca
Manglietia
Talauma singaporensis
Liriodendron tulipifera
Liriodendron chinensis*
Degeneria
Galbulimima
Eupomatia
Annona
Asimina
Cananga*
Knema
Cinnamomum
Persea
Hedycarya
Idiospermum
Calycanthus
Chimonanthus
Hernandia
Gyrocarpus*
monocots
Asarum
Saruma
Aristolochia
Lactoris*
Saururus
Houttuynia
Piper*
Peperomia
Ceratophyllum
Nymphaeaceae a
Barclayaceae a
Cabombaceae a
Amborellaceae c
Schisandraceae f
Illiciaceae f
Austrobaileyaceae b
Chloranthaceae d
Canellaceae b
Winteraceae b
Magnoliaceae b
Degeneriaceae b
Himantandraceae b
Eupomatiaceae b
Annonaceae b
Myristicaceae b
Lauraceae c
Monimiaceae c
Idiospermaceae c
Calycanthaceae c
Hernandiaceae c
Aristolochiaceae e
Lactoridaceae b
Saururaceae d
Piperaceae d
Ceratophyllaceae a
paleoherb II
Magnoliales
Laurales
paleoherb I
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
a Magnoliidae, Nyphaeales
b Magnoliidae, Magnoliales
c Magnoliidae, Laurales
d Magnoliidae, Piperales
e Magnoliidae, Aristolochiales
f Magnoliidae, Illiciales

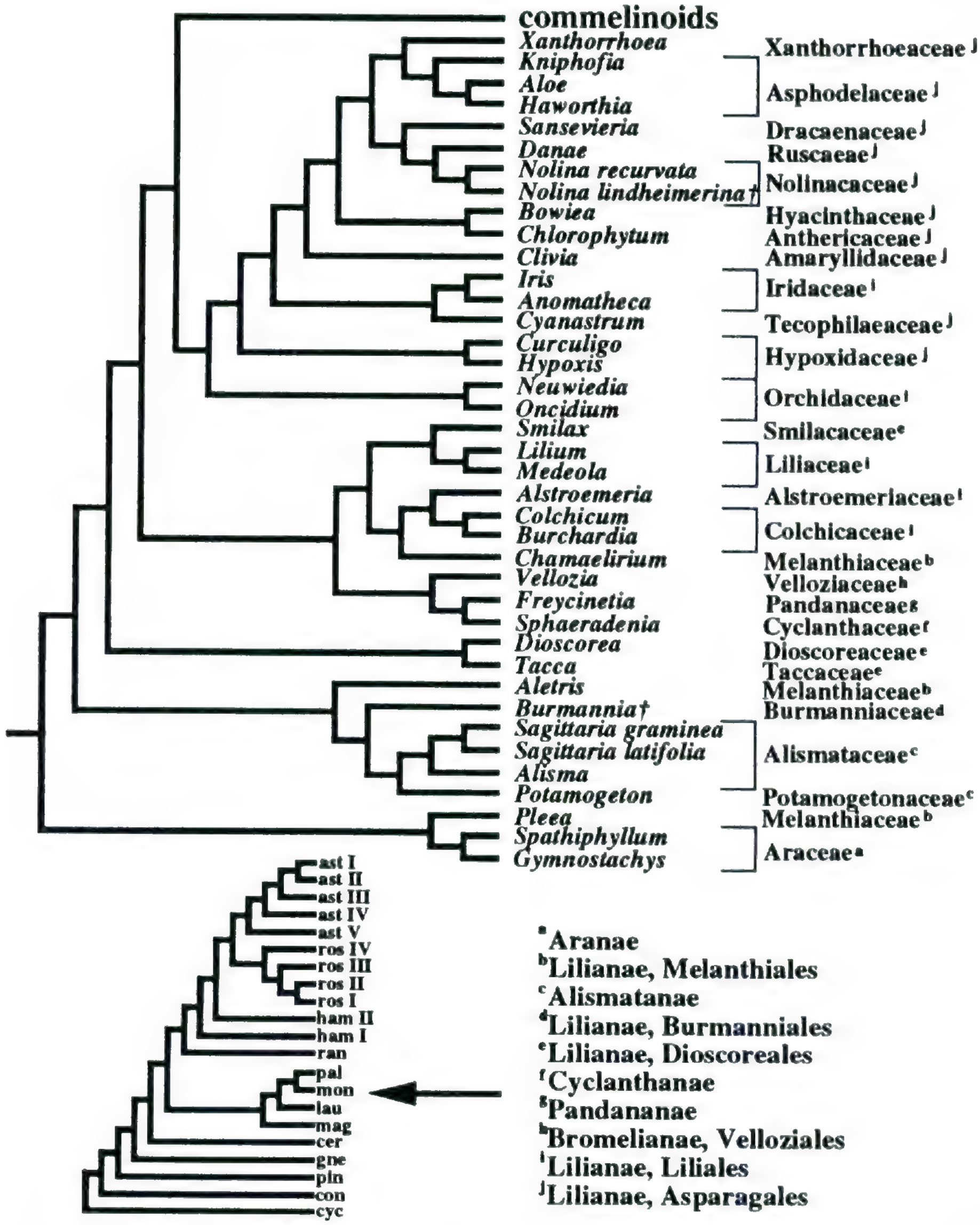
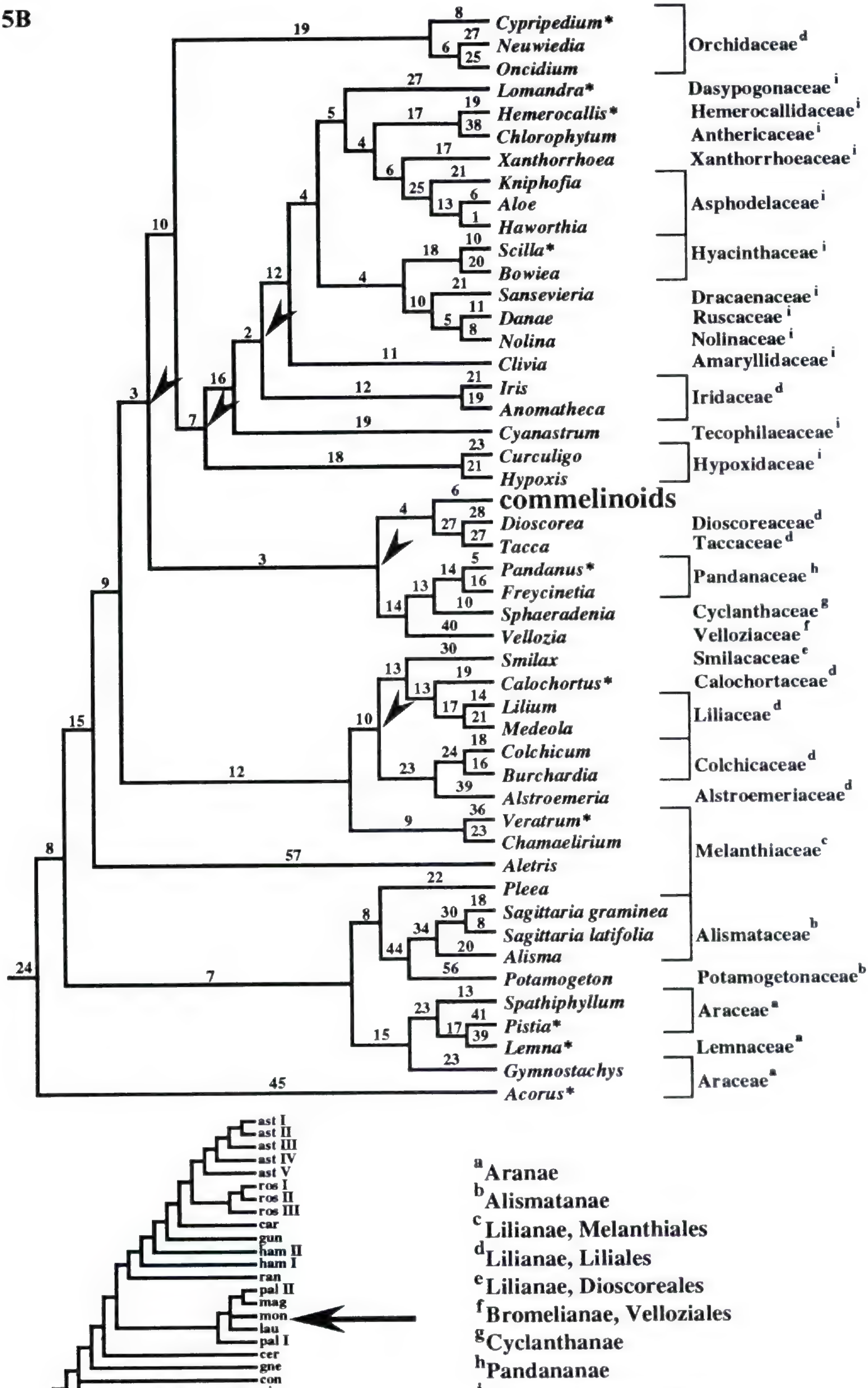



FIGURE 5. The five basalmost lineages of the monocots, composed of the aroids, alismatids, and lilioid groups. (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B were not available for Search I. Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

**5B**


Cypripedium*
Neuwiedia
Oncidium
Lomandra*
Hemerocallis*
Chlorophytum
Xanthorrhoea
Kniphofia
Aloe
Haworthia
Scilla*
Bowiea
Sansevieria
Danae
Nolina
Clivia
Iris
Anomatheca
Cyanastrum
Curculigo
Hypoxis
commelinoids
Dioscorea
Tacca
Pandanus*
Freycinetia
Sphaeradenia
Vellozia
Smilax
Calochortus*
Lilium
Medeola
Colchicum
Burchardia
Alstroemeria
Veratrum*
Chamaelirium
Aletris
Pleea
Sagittaria graminea
Sagittaria latifolia
Alisma
Potamogeton
Spathiphyllum
Pistia*
Lemna*
Gymnostachys
Acorus*
Orchidaceae[d]
Dasypogonaceae[i]
Hemerocallidaceae[i]
Anthericaceae[i]
Xanthorrhoeaceae[i]
Asphodelaceae[i]
Hyacinthaceae[i]
Dracaenaceae[i]
Ruscaceae[i]
Nolinaceae[i]
Amaryllidaceae[i]
Iridaceae[d]
Tecophilaeaceae[i]
Hypoxidaceae[i]
Dioscoreaceae[d]
Taccaceae[d]
Pandanaceae[h]
Cyclanthaceae[g]
Velloziaceae[f]
Smilacaceae[e]
Calochortaceae[d]
Liliaceae[d]
Colchicaceae[d]
Alstroemeriaceae[d]
Melanthiaceae[c]
Alismataceae[b]
Potamogetonaceae[b]
Araceae[a]
Lemnaceae[a]
Araceae[a]
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
[a]Aranae
[b]Alismatanae
[c]Lilianae, Melanthiales
[d]Lilianae, Liliales
[e]Lilianae, Dioscoreales
[f]Bromelianae, Velloziales
[g]Cyclanthanae
[h]Pandananae
[i]Lilianae, Asparagales

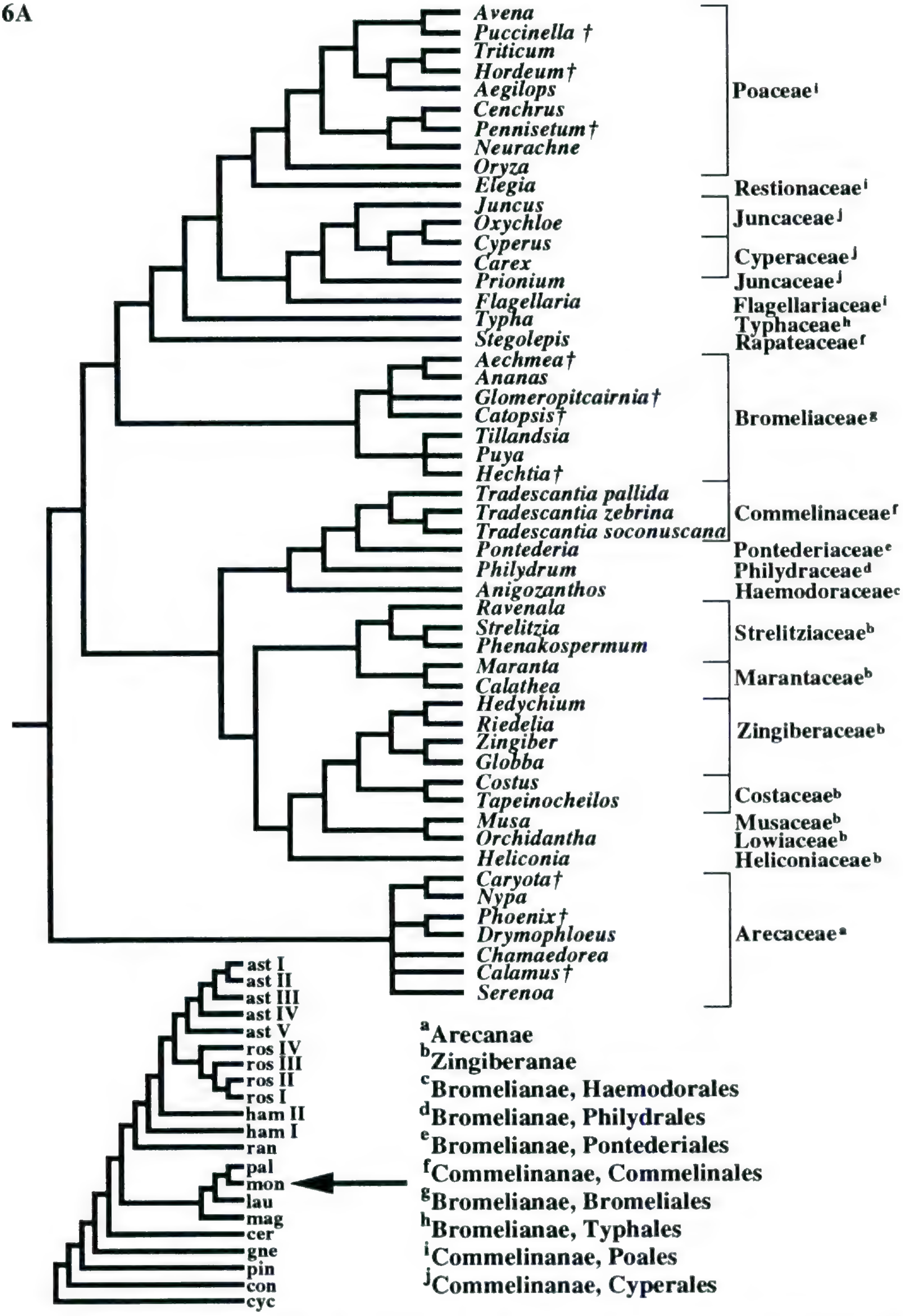
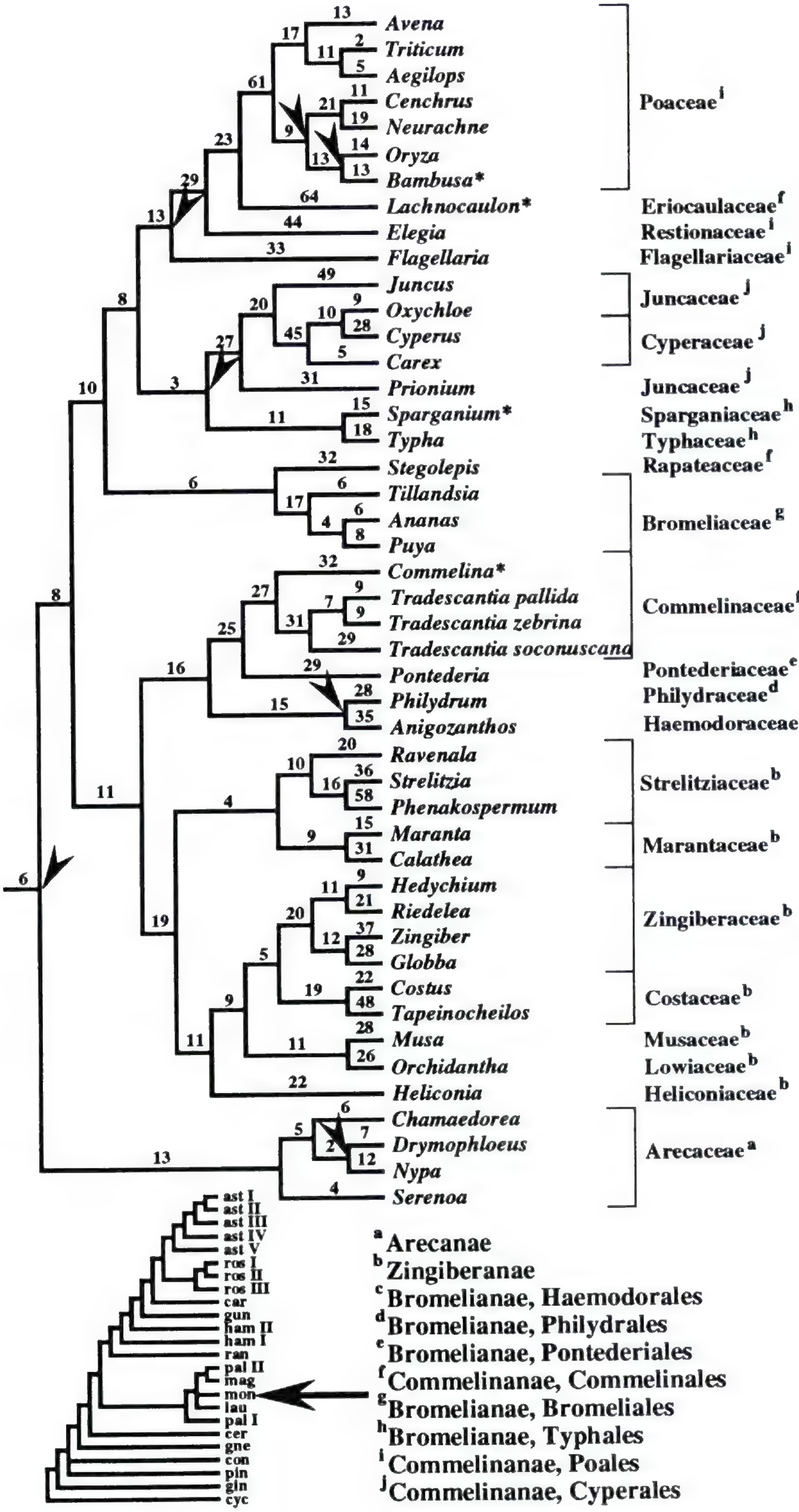



FIGURE 6. The terminal lineages of the monocots, composed of the palms, gingers, and commelinoids. (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B were not available for Search I. Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

**6B**


Avena
Triticum
Aegilops
Cenchrus
Neurachne
Oryza
Bambusa*
Lachnocaulon*
Elegia
Flagellaria
Juncus
Oxychloe
Cyperus
Carex
Prionium
Sparganium*
Typha
Stegolepis
Tillandsia
Ananas
Puya
Commelina*
Tradescantia pallida
Tradescantia zebrina
Tradescantia soconuscana
Pontederia
Philydrum
Anigozanthos
Ravenala
Strelitzia
Phenakospermum
Maranta
Calathea
Hedychium
Riedelea
Zingiber
Globba
Costus
Tapeinocheilos
Musa
Orchidantha
Heliconia
Chamaedorea
Drymophloeus
Nypa
Serenoa
Poaceae[i]
Eriocaulaceae[f]
Restionaceae[i]
Flagellariaceae[i]
Juncaceae[j]
Cyperaceae[j]
Juncaceae[j]
Sparganiaceae[h]
Typhaceae[h]
Rapateaceae[f]
Bromeliaceae[g]
Commelinaceae[f]
Pontederiaceae[e]
Philydraceae[d]
Haemodoraceae[c]
Strelitziaceae[b]
Marantaceae[b]
Zingiberaceae[b]
Costaceae[b]
Musaceae[b]
Lowiaceae[b]
Heliconiaceae[b]
Arecaceae[a]
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
[a] Arecanae
[b] Zingiberanae
[c] Bromelianae, Haemodorales
[d] Bromelianae, Philydrales
[e] Bromelianae, Pontederiales
[f] Commelinanae, Commelinales
[g] Bromelianae, Bromeliales
[h] Bromelianae, Typhales
[i] Commelinanae, Poales
[j] Commelinanae, Cyperales

7A

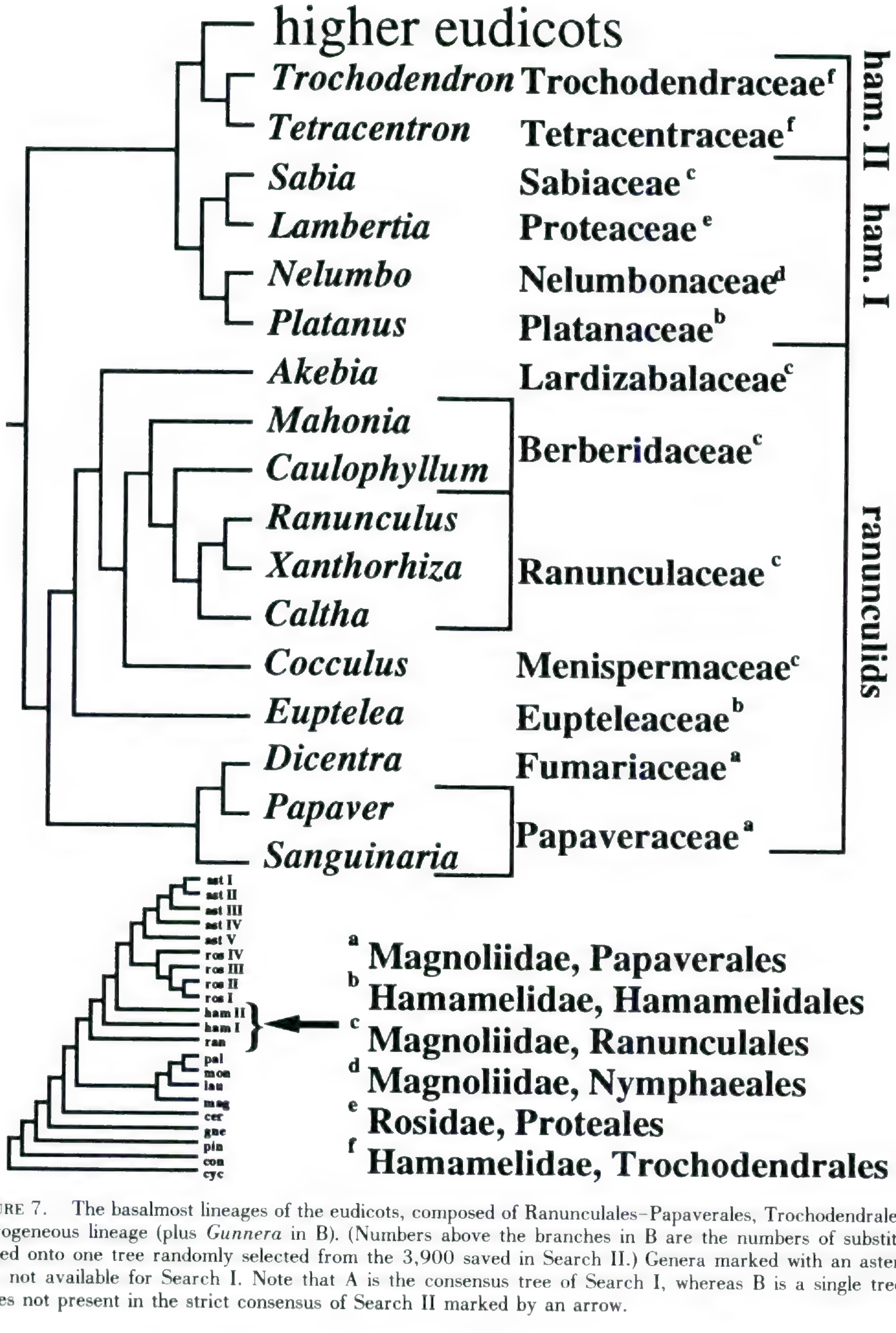
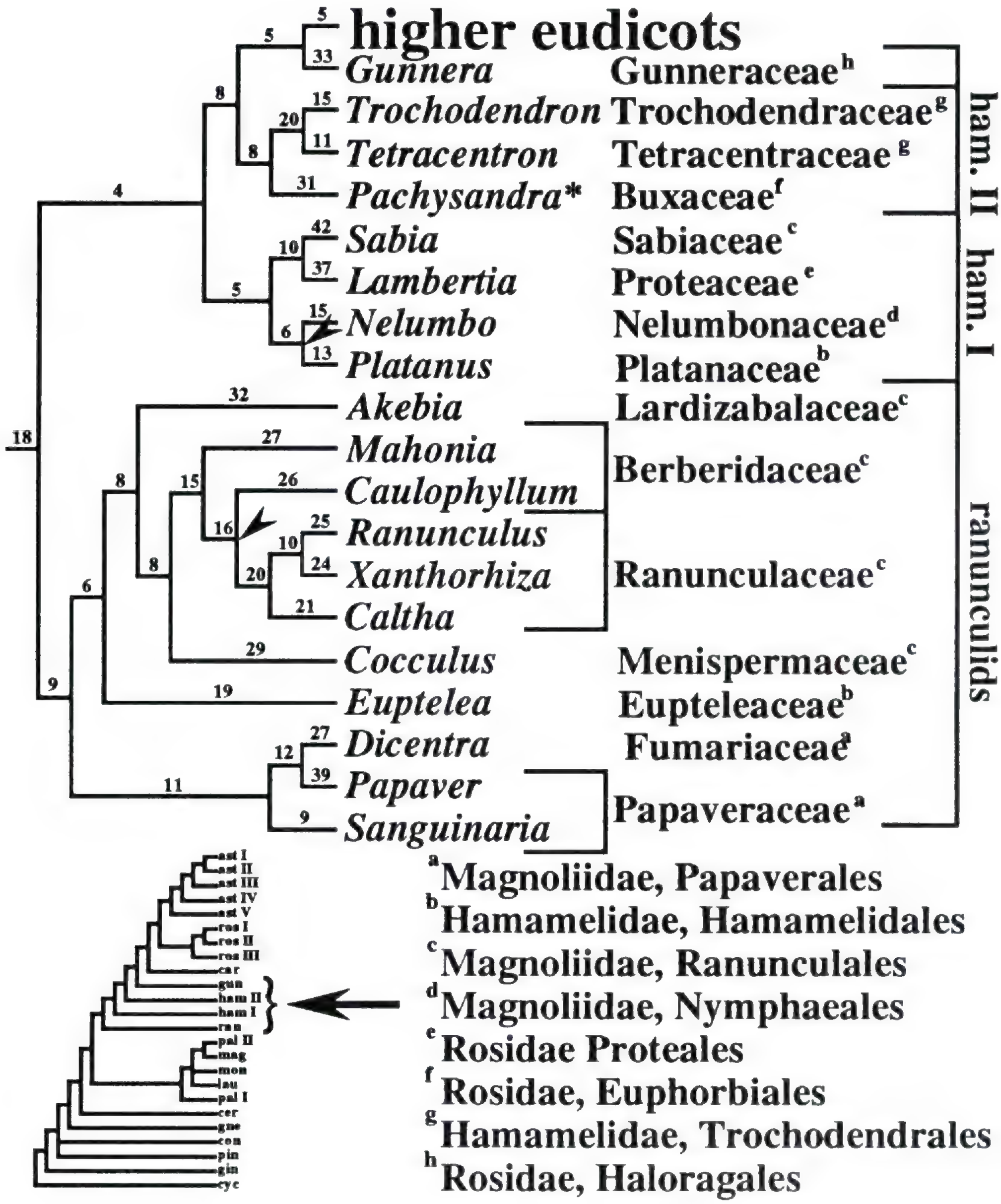



FIGURE 7. The basalmost lineages of the eudicots, composed of Ranunculales–Papaverales, Trochodendrales, and a heterogeneous lineage (plus *Gunnera* in B). (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with an asterisk in B were not available for Search I. Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

7B


higher eudicots
Gunnera Gunneraceae[h]
Trochodendron Trochodendraceae[g]
Tetracentron Tetracentraceae[g]
Pachysandra* Buxaceae[f]
Sabia Sabiaceae[c]
Lambertia Proteaceae[e]
Nelumbo Nelumbonaceae[d]
Platanus Platanaceae[b]
Akebia Lardizabalaceae[c]
Mahonia
Caulophyllum
Berberidaceae[c]
Ranunculus
Xanthorhiza
Caltha
Ranunculaceae[c]
Cocculus Menispermaceae[c]
Euptelea Eupteleaceae[b]
Dicentra Fumariaceae[a]
Papaver
Sanguinaria
Papaveraceae[a]
ham. II
ham. I
ranunculids
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
[a]Magnoliidae, Papaverales
[b]Hamamelidae, Hamamelidales
[c]Magnoliidae, Ranunculales
[d]Magnoliidae, Nymphaeales
[e]Rosidae Proteales
[f]Rosidae, Euphorbiales
[g]Hamamelidae, Trochodendrales
[h]Rosidae, Haloragales

8A

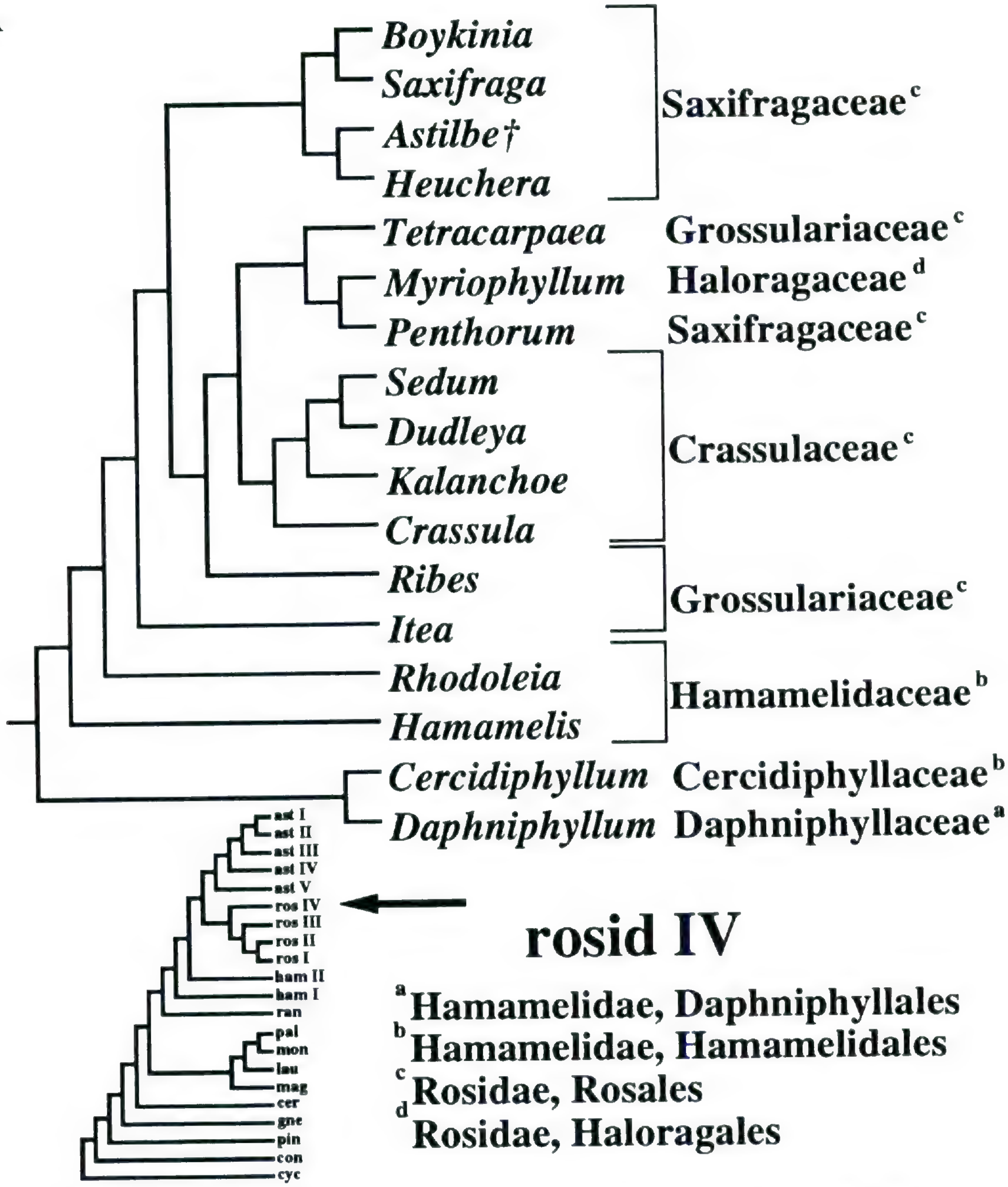
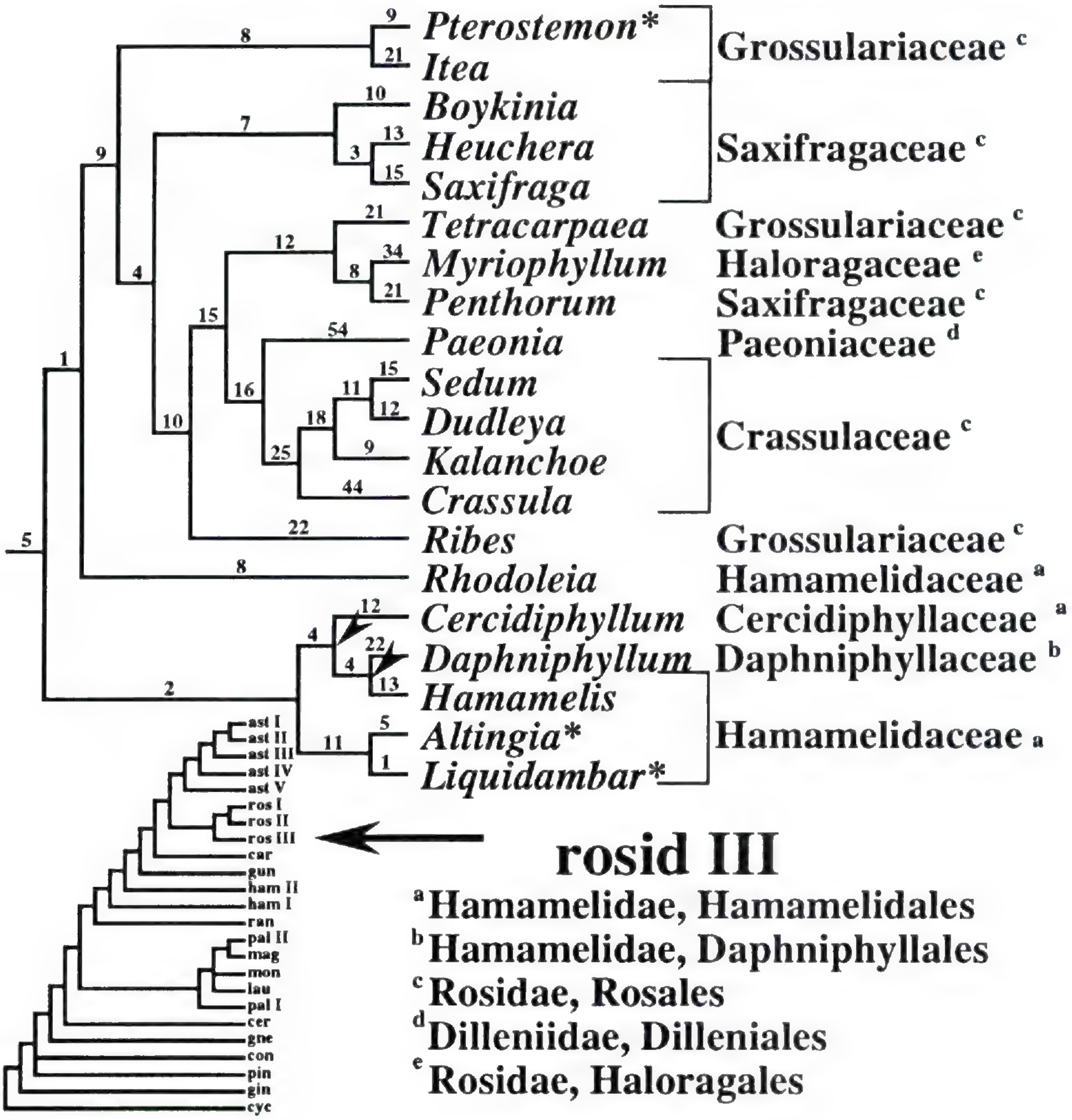



FIGURE 8. The basalmost lineage of rosid dicots, which includes a number of lower hamamelids. (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B were not available for Search I. Note that the positions of this clade and that of the Caryophyllidae (Fig. 9A, B) differ significantly in the results of Searches I and II (see Figs. 1, 2). Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

**8B**


Pterostemon*
Itea
Boykinia
Heuchera
Saxifraga
Tetracarpaea
Myriophyllum
Penthorum
Paeonia
Sedum
Dudleya
Kalanchoe
Crassula
Ribes
Rhodoleia
Cercidiphyllum
Daphniphyllum
Hamamelis
Altingia*
Liquidambar*
Grossulariaceae c
Saxifragaceae c
Grossulariaceae c
Haloragaceae e
Saxifragaceae c
Paeoniaceae d
Crassulaceae c
Grossulariaceae c
Hamamelidaceae a
Cercidiphyllaceae a
Daphniphyllaceae b
Hamamelidaceae a
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
rosid III
[a]Hamamelidae, Hamamelidales
[b]Hamamelidae, Daphniphyllales
[c]Rosidae, Rosales
[d]Dilleniidae, Dilleniales
[e]Rosidae, Haloragales

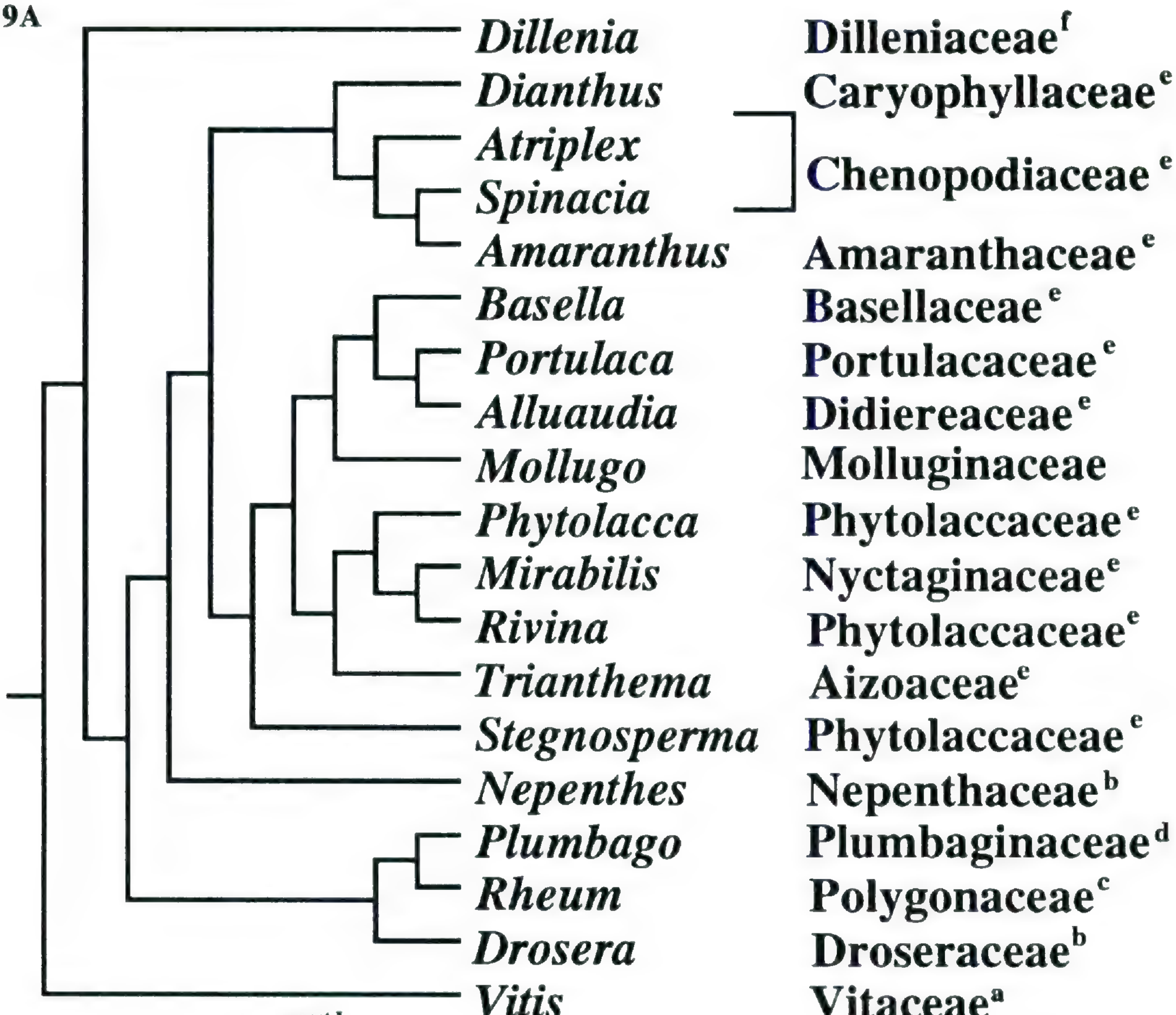
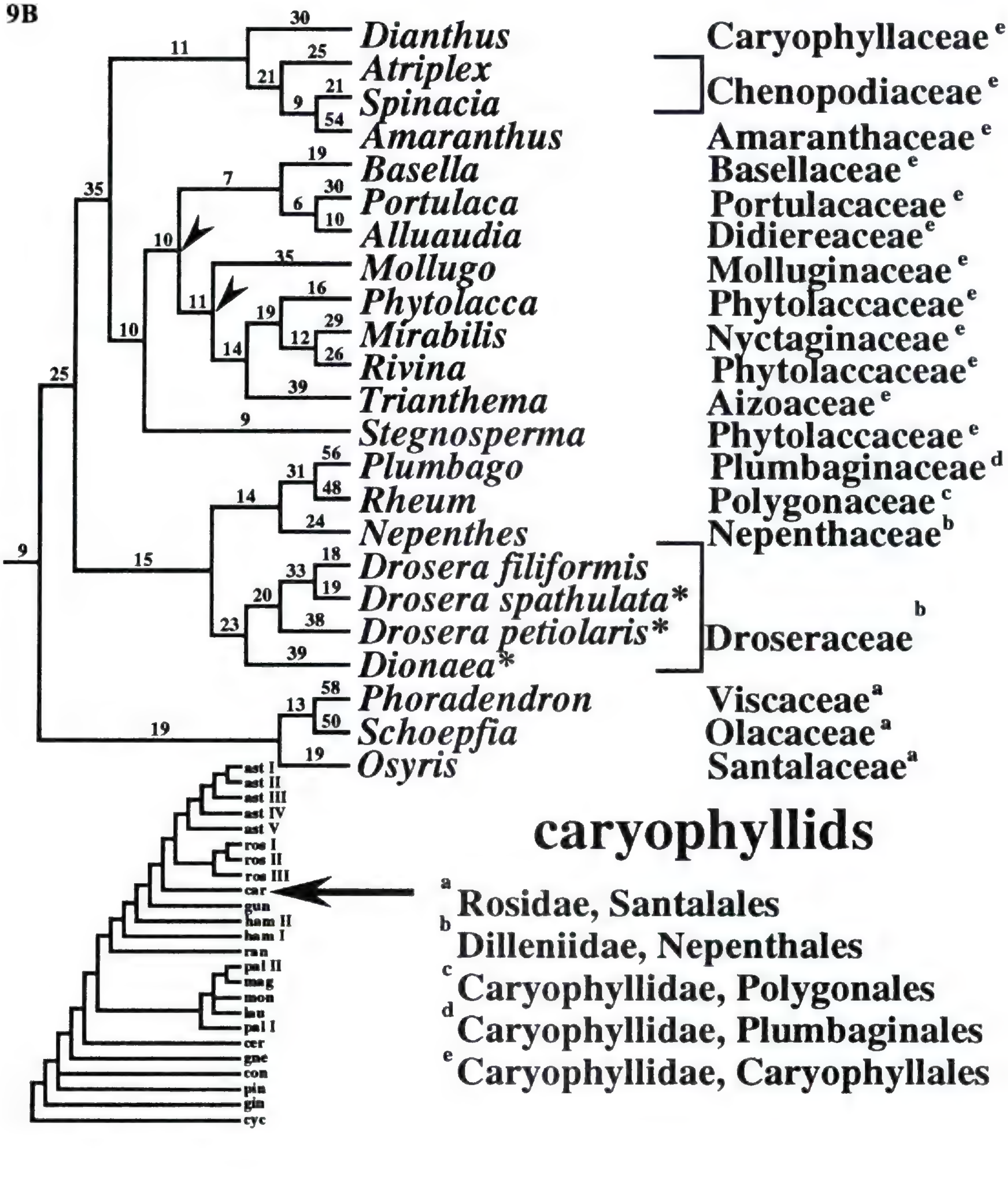



FIGURE 9. The lineage that includes the Caryophyllidae. (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with an asterisk in B were not available for Search I. Note that the positions of this clade and that of rosid IV (Fig. 8A, B) differ significantly in the results of Searches I and II (see Figs. 1, 2). Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

**9B**


Dianthus
Atriplex
Spinacia
Amaranthus
Basella
Portulaca
Alluaudia
Mollugo
Phytolacca
Mirabilis
Rivina
Trianthema
Stegnosperma
Plumbago
Rheum
Nepenthes
Drosera filiformis
Drosera spathulata*
Drosera petiolaris*
Dionaea*
Phoradendron
Schoepfia
Osyris
Caryophyllaceae e
Chenopodiaceae e
Amaranthaceae e
Basellaceae e
Portulacaceae e
Didiereaceae e
Molluginaceae e
Phytolaccaceae e
Nyctaginaceae e
Phytolaccaceae e
Aizoaceae e
Phytolaccaceae e
Plumbaginaceae d
Polygonaceae c
Nepenthaceae b
Droseraceae b
Viscaceae a
Olacaceae a
Santalaceae a
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
caryophyllids
a Rosidae, Santalales
b Dilleniidae, Nepenthales
c Caryophyllidae, Polygonales
d Caryophyllidae, Plumbaginales
e Caryophyllidae, Caryophyllales

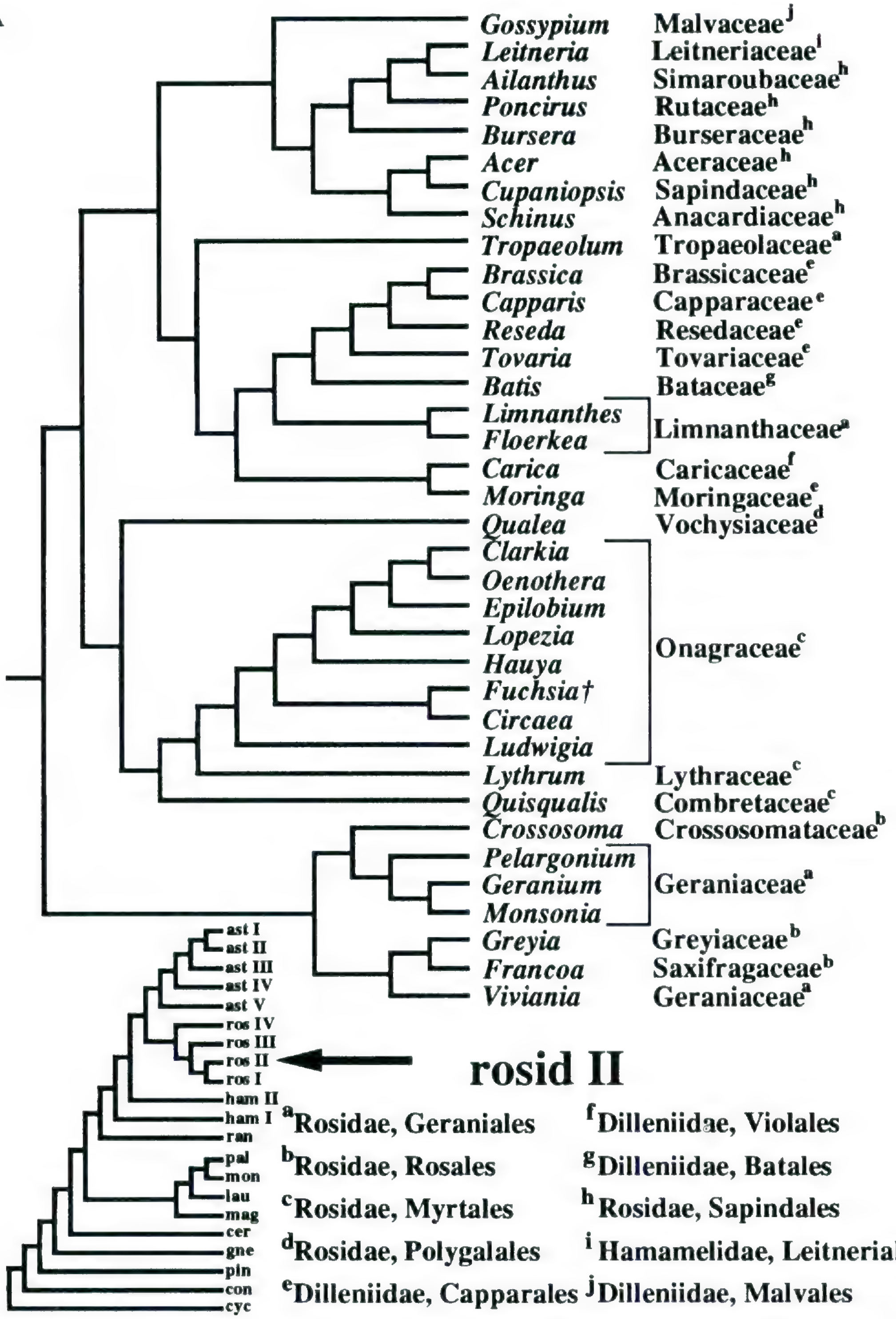
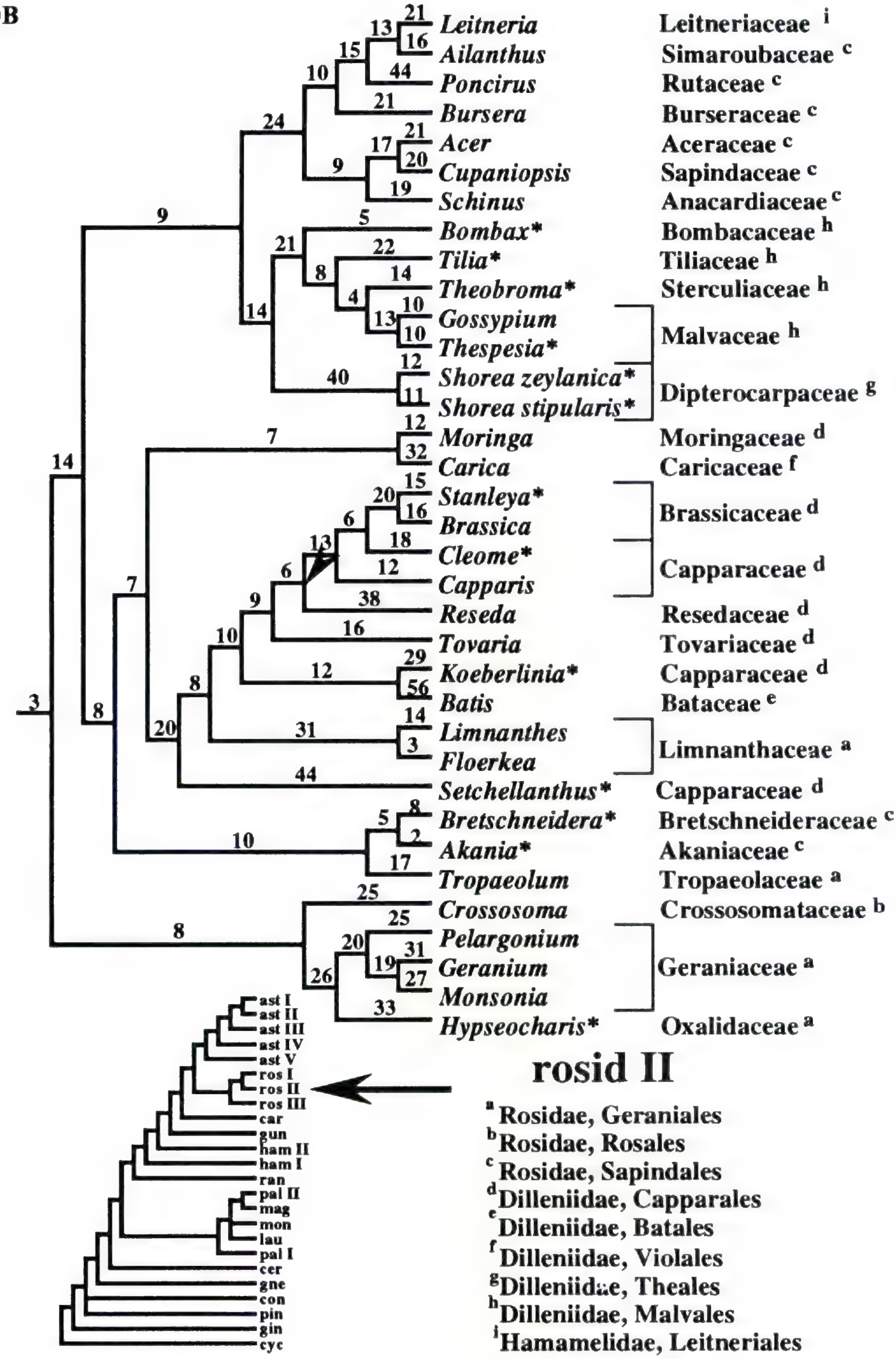



FIGURE 10. One of the two "higher" rosid lineages. (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B were not available for Search I. Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

**10B**




[a] Rosidae, Geraniales
[b] Rosidae, Rosales
[c] Rosidae, Sapindales
[d] Dilleniidae, Capparales
[e] Dilleniidae, Batales
[f] Dilleniidae, Violales
[g] Dilleniidae, Theales
[h] Dilleniidae, Malvales
[i] Hamamelidae, Leitneriales

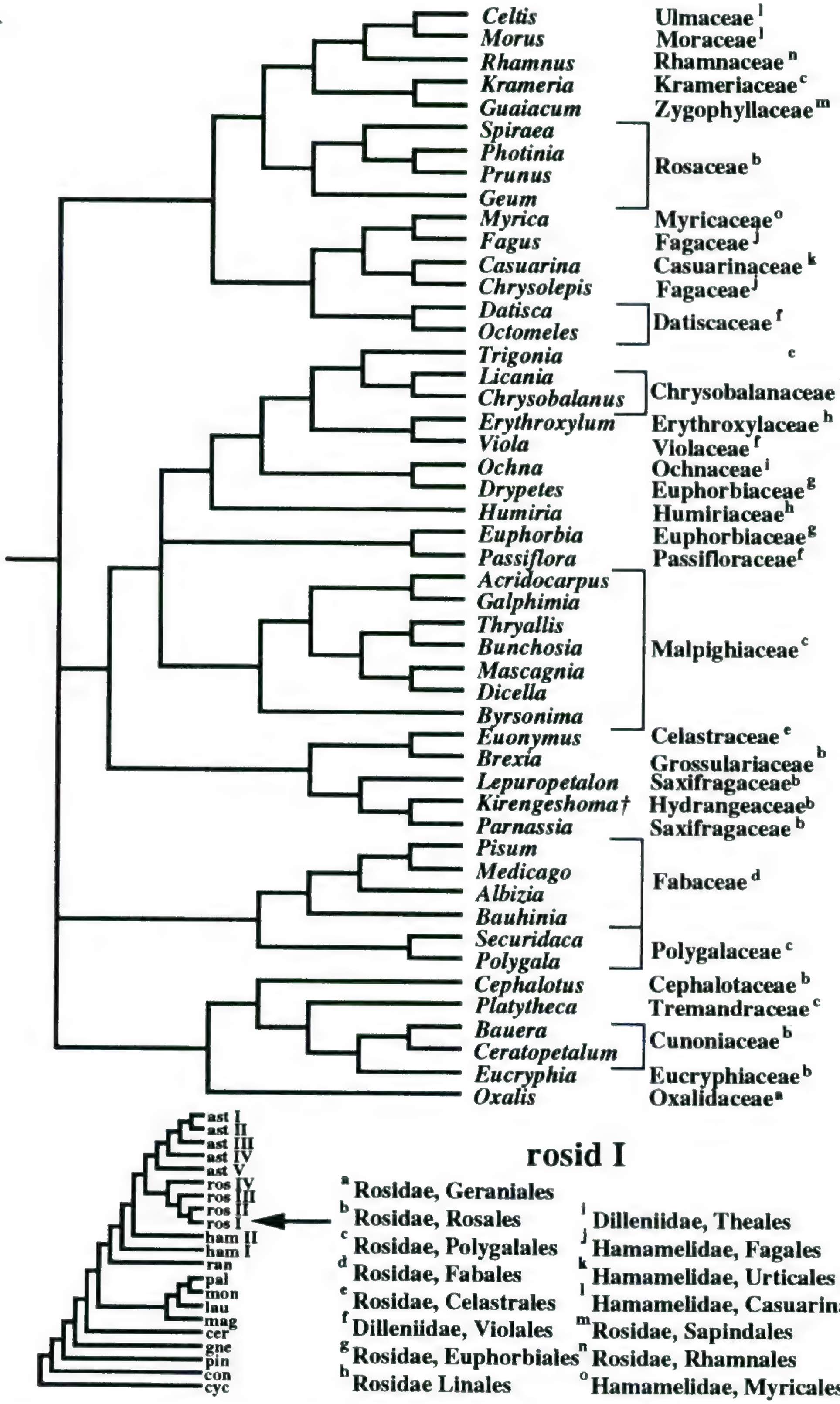
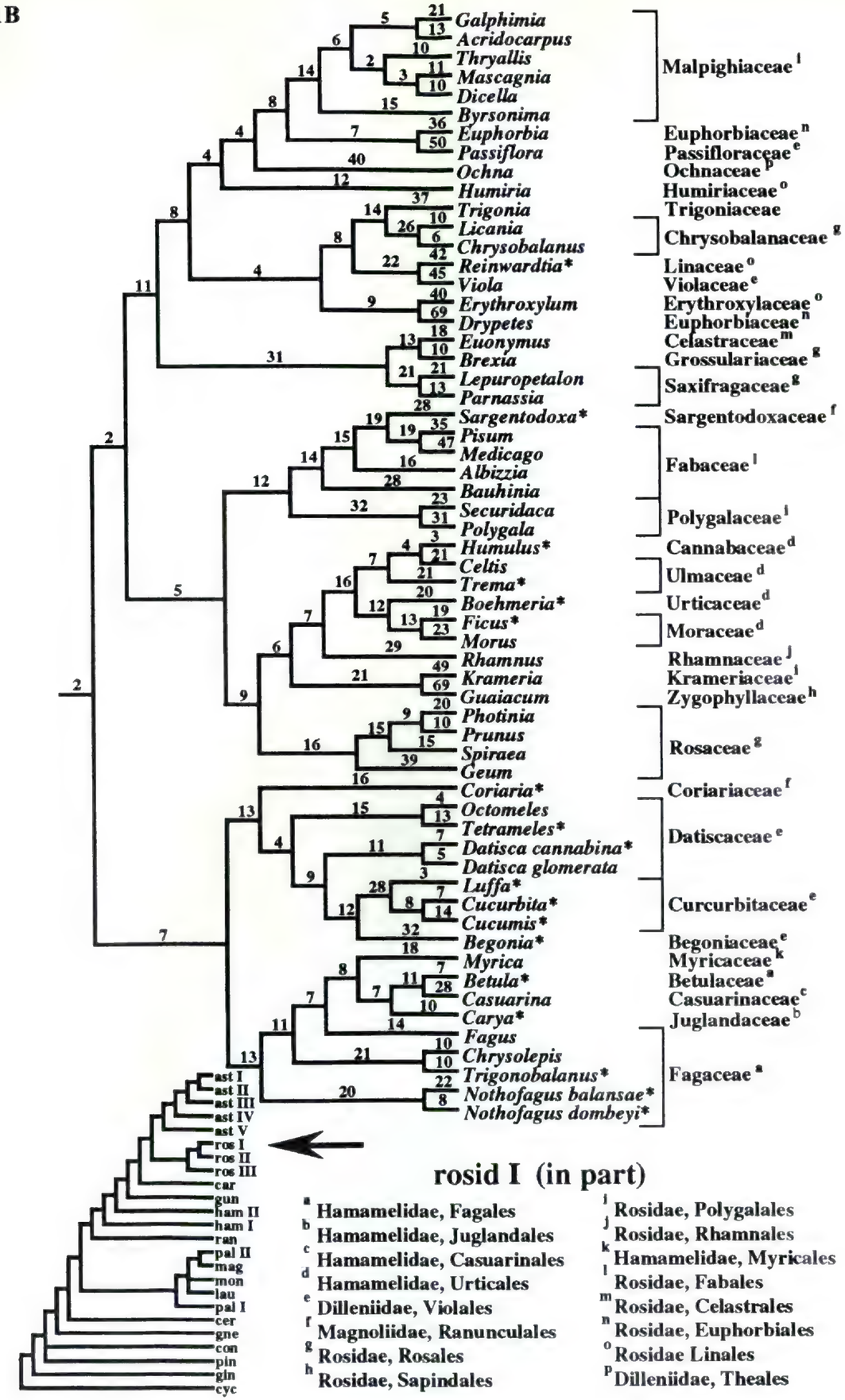



FIGURE 11. The second "higher" rosid lineage. (Numbers above the branches in B and C, see foldout, are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B and C were not available for Search I. The taxon labeled "*Kirengoshoma*" was, subsequent to Search I, discovered to be misidentified and was removed from Search II; its identity is unknown. Note that A is the consensus tree of Search I, whereas B and C are a single tree with branches not present in the strict consensus of Search II marked by an arrow.

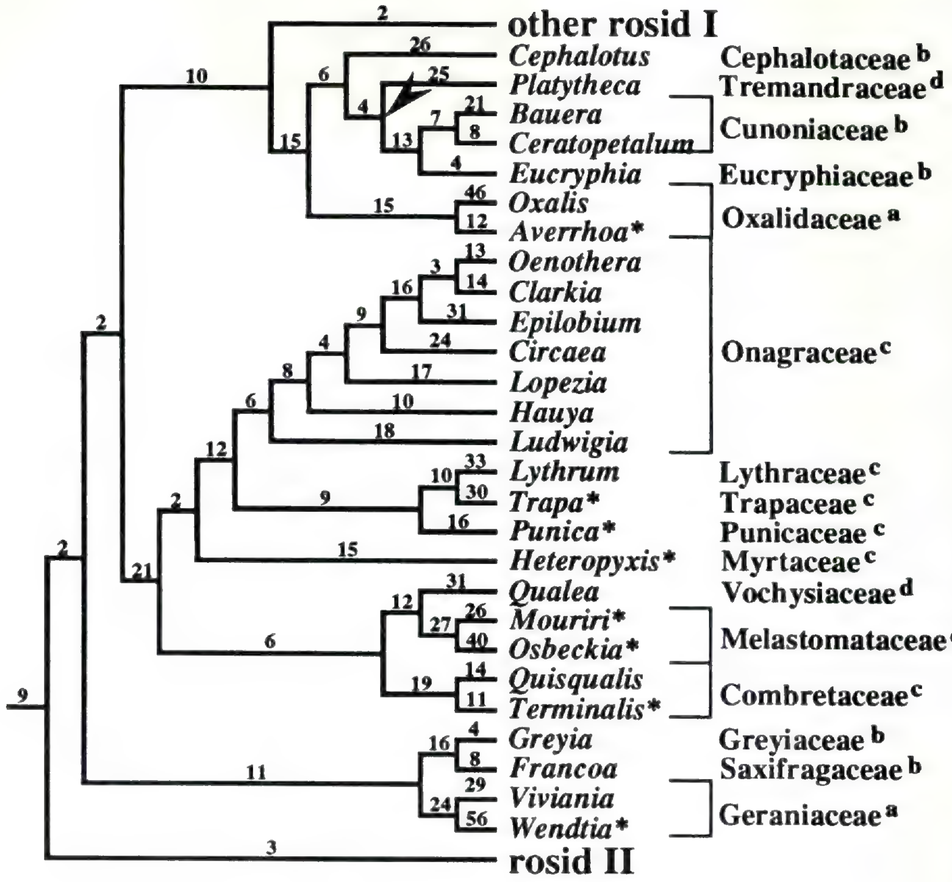
11B

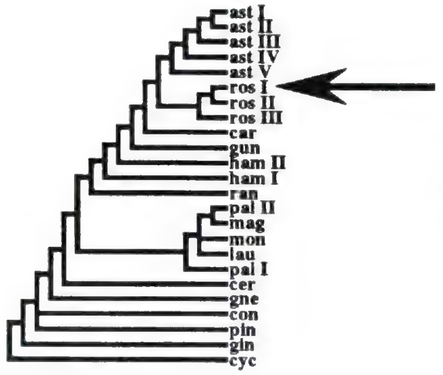



rosid I (in part)

a Hamamelidae, Fagales
b Hamamelidae, Juglandales
c Hamamelidae, Casuarinales
d Hamamelidae, Urticales
e Dilleniidae, Violales
f Magnoliidae, Ranunculales
g Rosidae, Rosales
h Rosidae, Sapindales
i Rosidae, Polygalales
j Rosidae, Rhamnales
k Hamamelidae, Myricales
l Rosidae, Fabales
m Rosidae, Celastrales
n Rosidae, Euphorbiales
o Rosidae Linales
p Dilleniidae, Theales

11C




rosid I (in part)

a Rosidae, Geraniales
b Rosidae, Rosales
c Rosidae, Myrtales
d Rosidae, Polygalales

12A

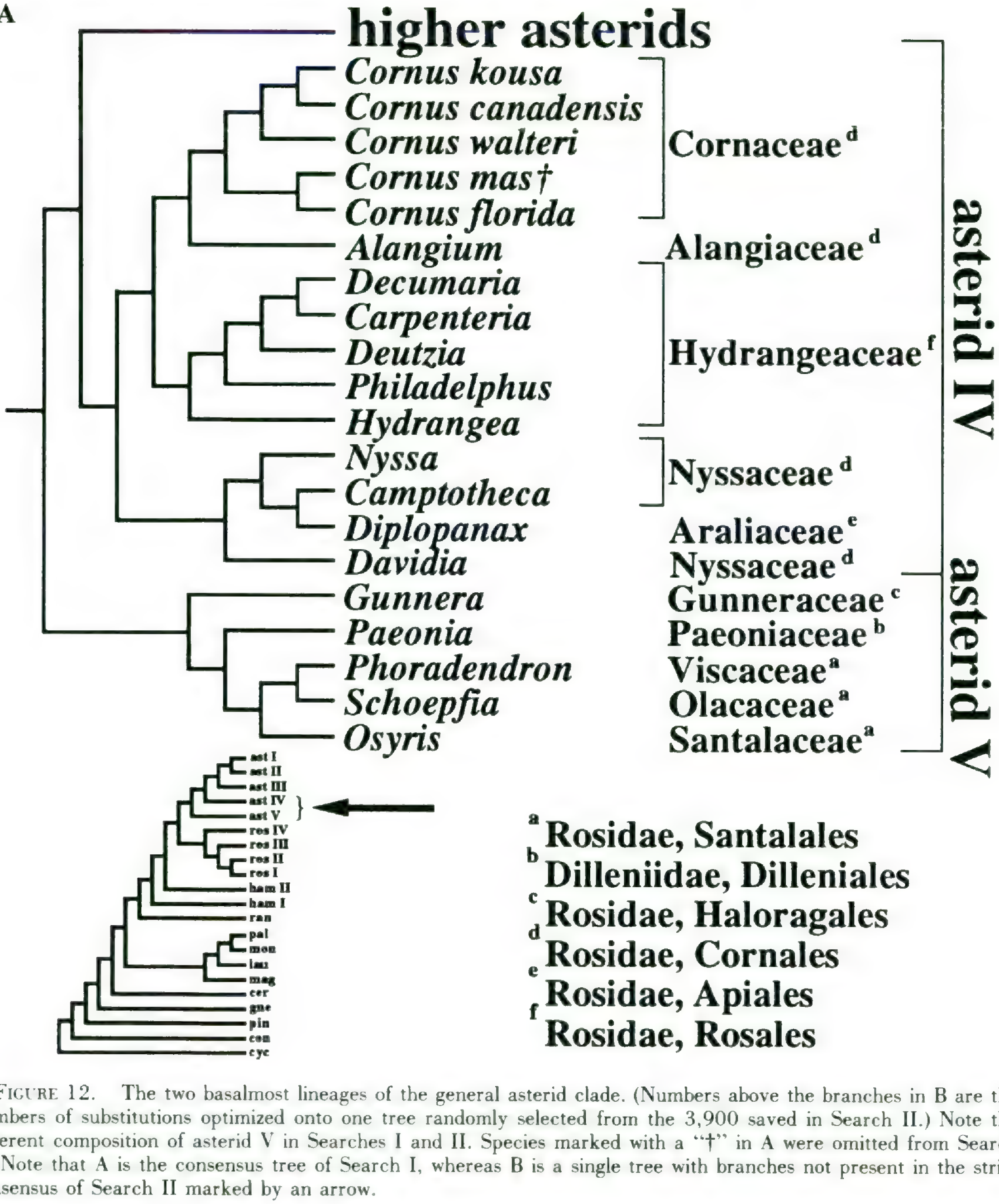
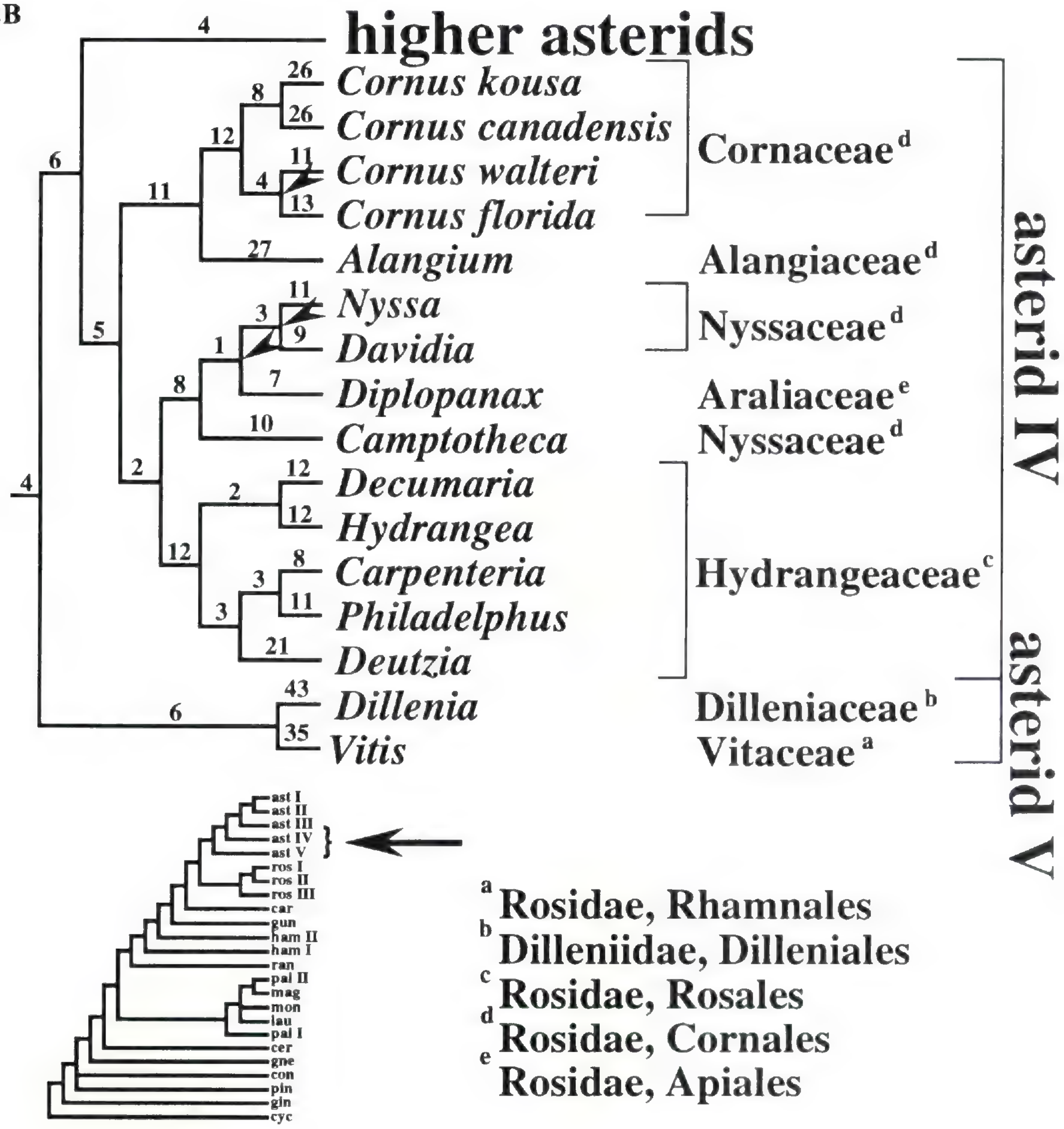



FIGURE 12. The two basalmost lineages of the general asterid clade. (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Note the different composition of asterid V in Searches I and II. Species marked with a "†" in A were omitted from Search II. Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.


12B
higher asterids
Cornus kousa
Cornus canadensis
Cornus walteri
Cornus florida
Alangium
Nyssa
Davidia
Diplopanax
Camptotheca
Decumaria
Hydrangea
Carpenteria
Philadelphus
Deutzia
Dillenia
Vitis
Cornaceae[d]
Alangiaceae[d]
Nyssaceae[d]
Araliaceae[e]
Nyssaceae[d]
Hydrangeaceae[c]
Dilleniaceae[b]
Vitaceae[a]
asterid IV
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
[a] Rosidae, Rhamnales
[b] Dilleniidae, Dilleniales
[c] Rosidae, Rosales
[d] Rosidae, Cornales
[e] Rosidae, Apiales

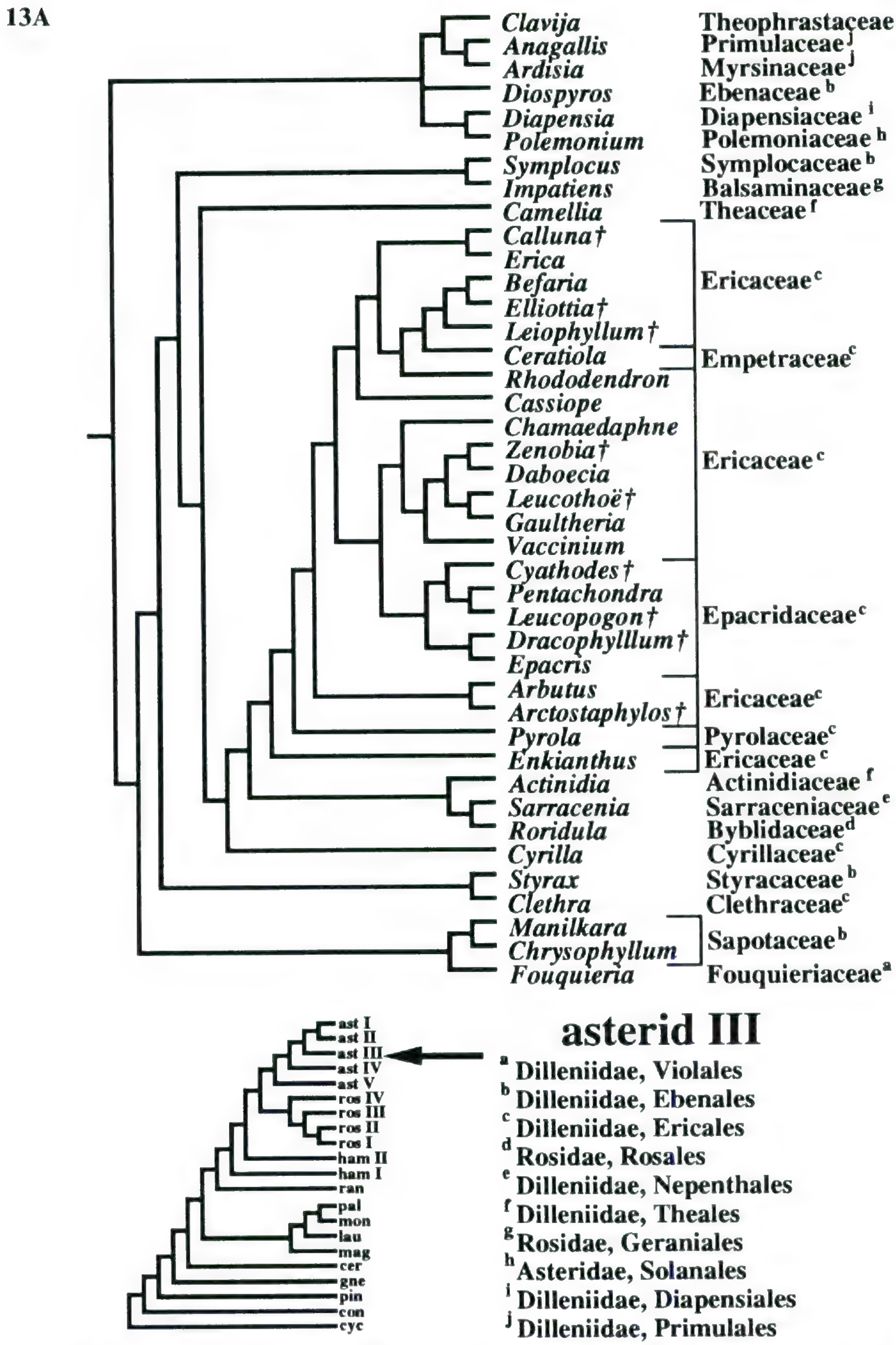
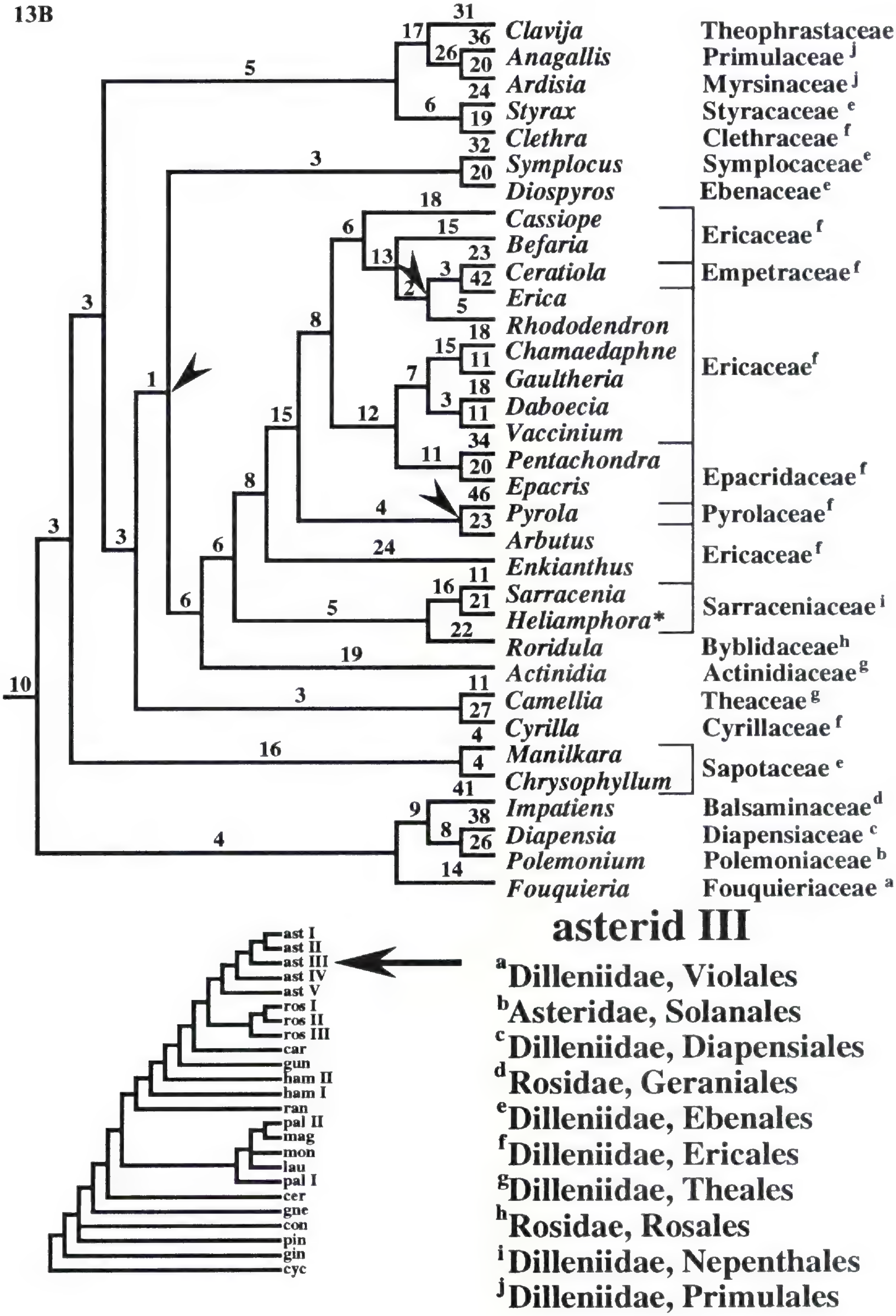
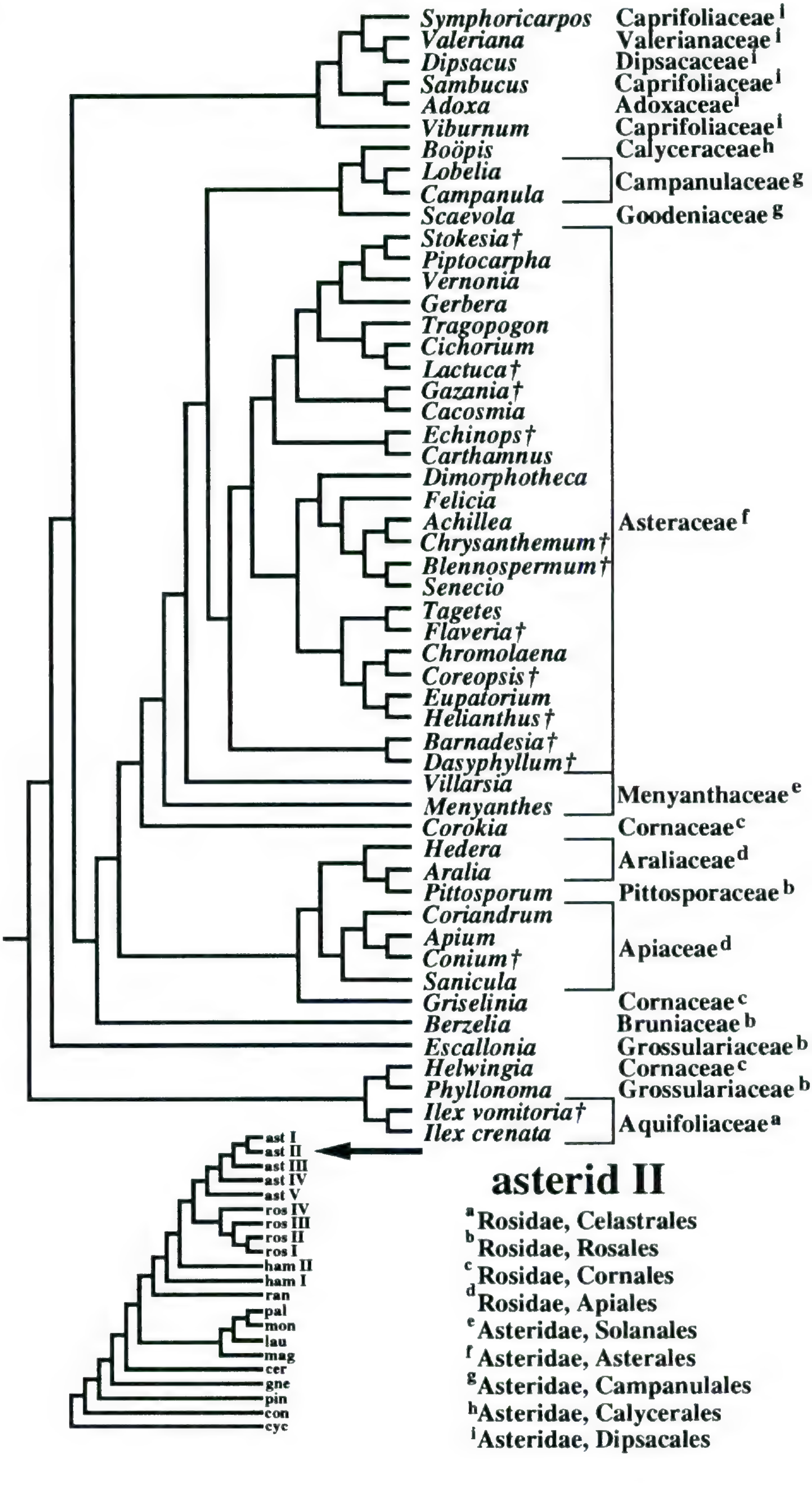



FIGURE 13. The immediate sister lineage to the clade composed of traditional asterids. (Numbers above the branches are the numbers of substitutions optimized on the general semi-strict consensus tree in A and one tree randomly selected from the 3,900 saved in B.) Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B were not available for Search I. Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

**13B**


31
17
36
26
20
24
6
19
32
3
20
18
6
15
13
23
3
42
2
5
8
18
15
11
7
18
3
11
12
15
34
11
20
8
46
4
23
6
24
11
16
21
5
22
19
11
3
27
4
16
4
41
9
38
8
26
4
14
Clavija
Anagallis
Ardisia
Styrax
Clethra
Symplocus
Diospyros
Cassiope
Befaria
Ceratiola
Erica
Rhododendron
Chamaedaphne
Gaultheria
Daboecia
Vaccinium
Pentachondra
Epacris
Pyrola
Arbutus
Enkianthus
Sarracenia
Heliamphora*
Roridula
Actinidia
Camellia
Cyrilla
Manilkara
Chrysophyllum
Impatiens
Diapensia
Polemonium
Fouquieria
Theophrastaceae j
Primulaceae j
Myrsinaceae j
Styracaceae e
Clethraceae f
Symplocaceae e
Ebenaceae e
Ericaceae f
Empetraceae f
Ericaceae f
Epacridaceae f
Pyrolaceae f
Ericaceae f
Sarraceniaceae i
Byblidaceae h
Actinidiaceae g
Theaceae g
Cyrillaceae f
Sapotaceae e
Balsaminaceae d
Diapensiaceae c
Polemoniaceae b
Fouquieriaceae a
asterid III
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
a Dilleniidae, Violales
b Asteridae, Solanales
c Dilleniidae, Diapensiales
d Rosidae, Geraniales
e Dilleniidae, Ebenales
f Dilleniidae, Ericales
g Dilleniidae, Theales
h Rosidae, Rosales
i Dilleniidae, Nepenthales
j Dilleniidae, Primulales

14A




**asterid II**

[a] Rosidae, Celastrales
[b] Rosidae, Rosales
[c] Rosidae, Cornales
[d] Rosidae, Apiales
[e] Asteridae, Solanales
[f] Asteridae, Asterales
[g] Asteridae, Campanulales
[h] Asteridae, Calycerales
[i] Asteridae, Dipsacales

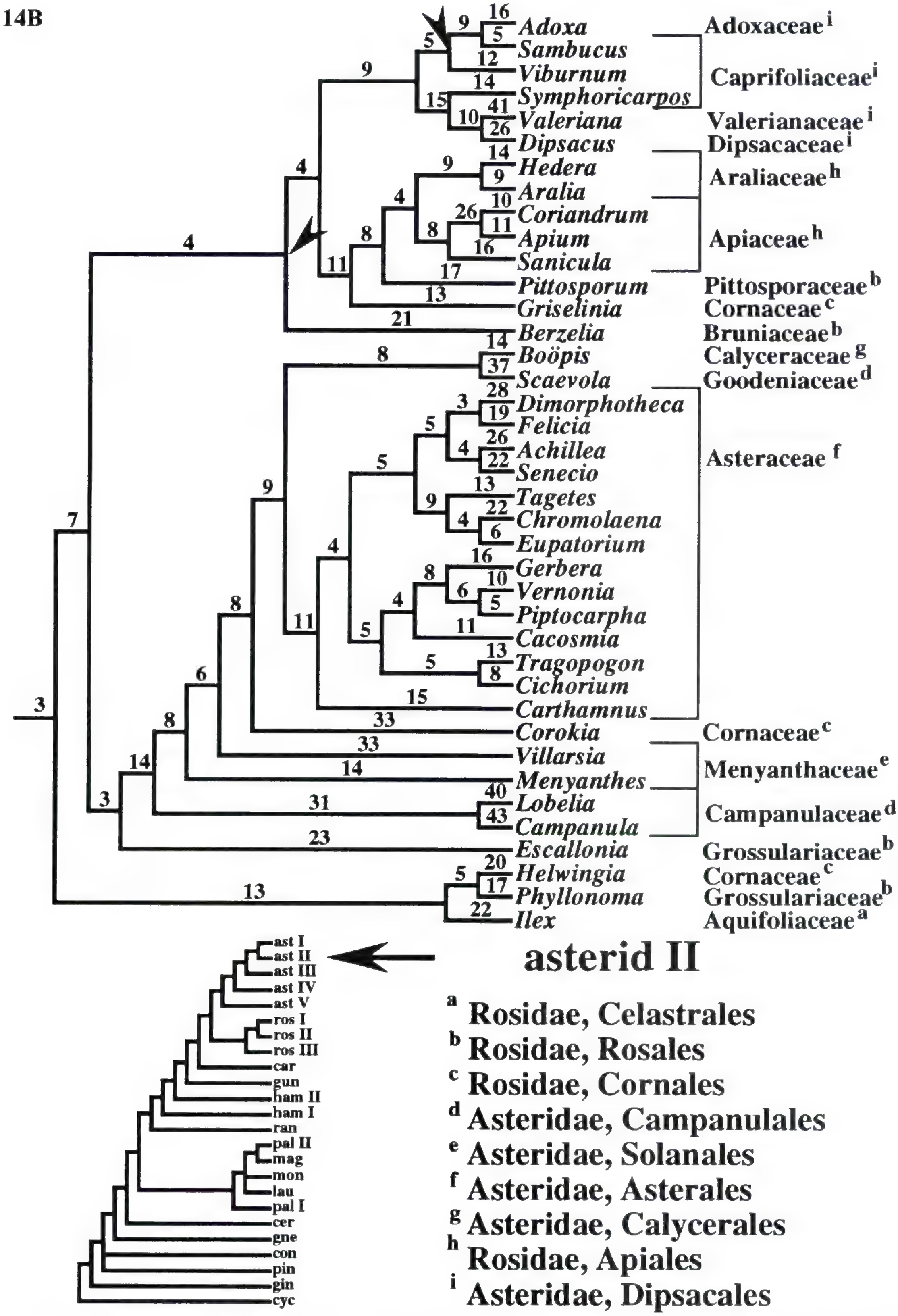



FIGURE 14. One of the two clades of traditional Asteridae. (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with a "†" in A were omitted from Search II. Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

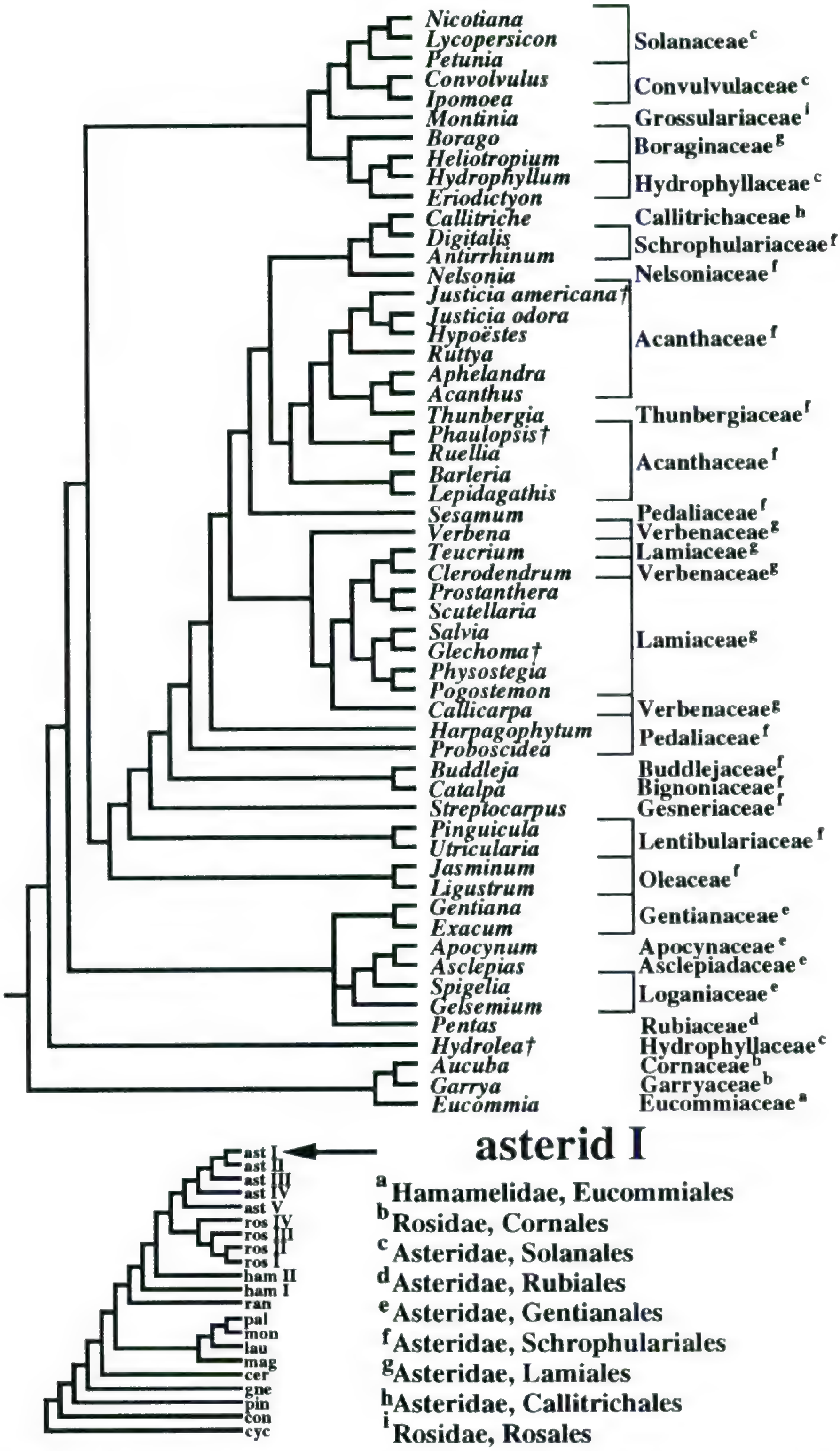
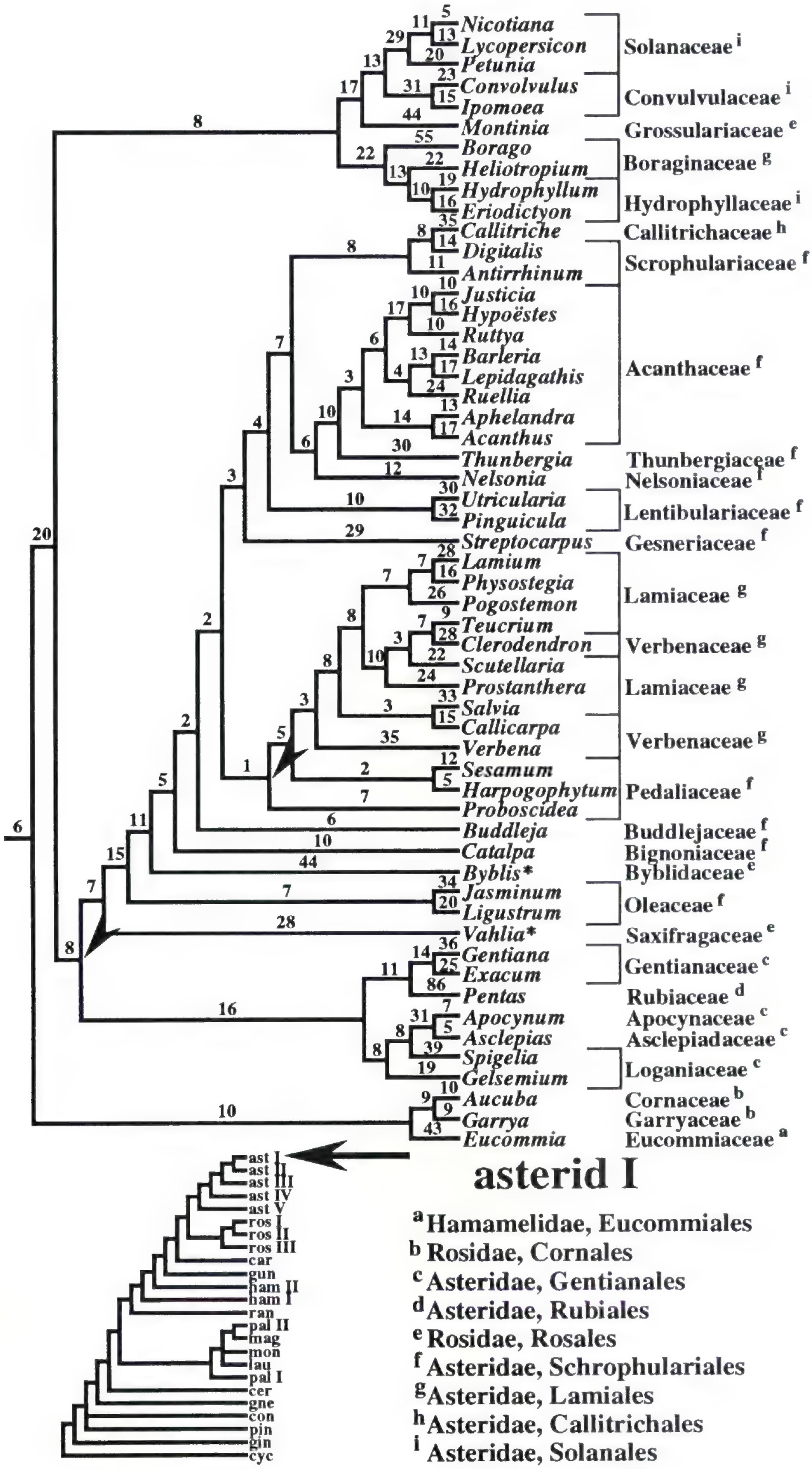



FIGURE 15. The second clade of traditional Asteridae. (Numbers above the branches in B are the numbers of substitutions optimized onto one tree randomly selected from the 3,900 saved in Search II.) Genera marked with a "†" in A were omitted from Search II; genera marked with an asterisk in B were not available for Search I. Note that A is the consensus tree of Search I, whereas B is a single tree with branches not present in the strict consensus of Search II marked by an arrow.

**15B**


Nicotiana
Lycopersicon
Petunia
Convolvulus
Ipomoea
Montinia
Borago
Heliotropium
Hydrophyllum
Eriodictyon
Callitriche
Digitalis
Antirrhinum
Justicia
Hypoëstes
Ruttya
Barleria
Lepidagathis
Ruellia
Aphelandra
Acanthus
Thunbergia
Nelsonia
Utricularia
Pinguicula
Streptocarpus
Lamium
Physostegia
Pogostemon
Teucrium
Clerodendron
Scutellaria
Prostanthera
Salvia
Callicarpa
Verbena
Sesamum
Harpogophytum
Proboscidea
Buddleja
Catalpa
Byblis*
Jasminum
Ligustrum
Vahlia*
Gentiana
Exacum
Pentas
Apocynum
Asclepias
Spigelia
Gelsemium
Aucuba
Garrya
Eucommia
Solanaceae i
Convulvulaceae i
Grossulariaceae e
Boraginaceae g
Hydrophyllaceae i
Callitrichaceae h
Scrophulariaceae f
Acanthaceae f
Thunbergiaceae f
Nelsoniaceae f
Lentibulariaceae f
Gesneriaceae f
Lamiaceae g
Verbenaceae g
Lamiaceae g
Verbenaceae g
Pedaliaceae f
Buddlejaceae f
Bignoniaceae f
Byblidaceae e
Oleaceae f
Saxifragaceae e
Gentianaceae c
Rubiaceae d
Apocynaceae c
Asclepiadaceae c
Loganiaceae c
Cornaceae b
Garryaceae b
Eucommiaceae a
ast I
ast II
ast III
ast IV
ast V
ros I
ros II
ros III
car
gun
ham II
ham I
ran
pal II
mag
mon
lau
pal I
cer
gne
con
pin
gin
cyc
asterid I
a Hamamelidae, Eucommiales
b Rosidae, Cornales
c Asteridae, Gentianales
d Asteridae, Rubiales
e Rosidae, Rosales
f Asteridae, Schrophulariales
g Asteridae, Lamiales
h Asteridae, Callitrichales
i Asteridae, Solanales

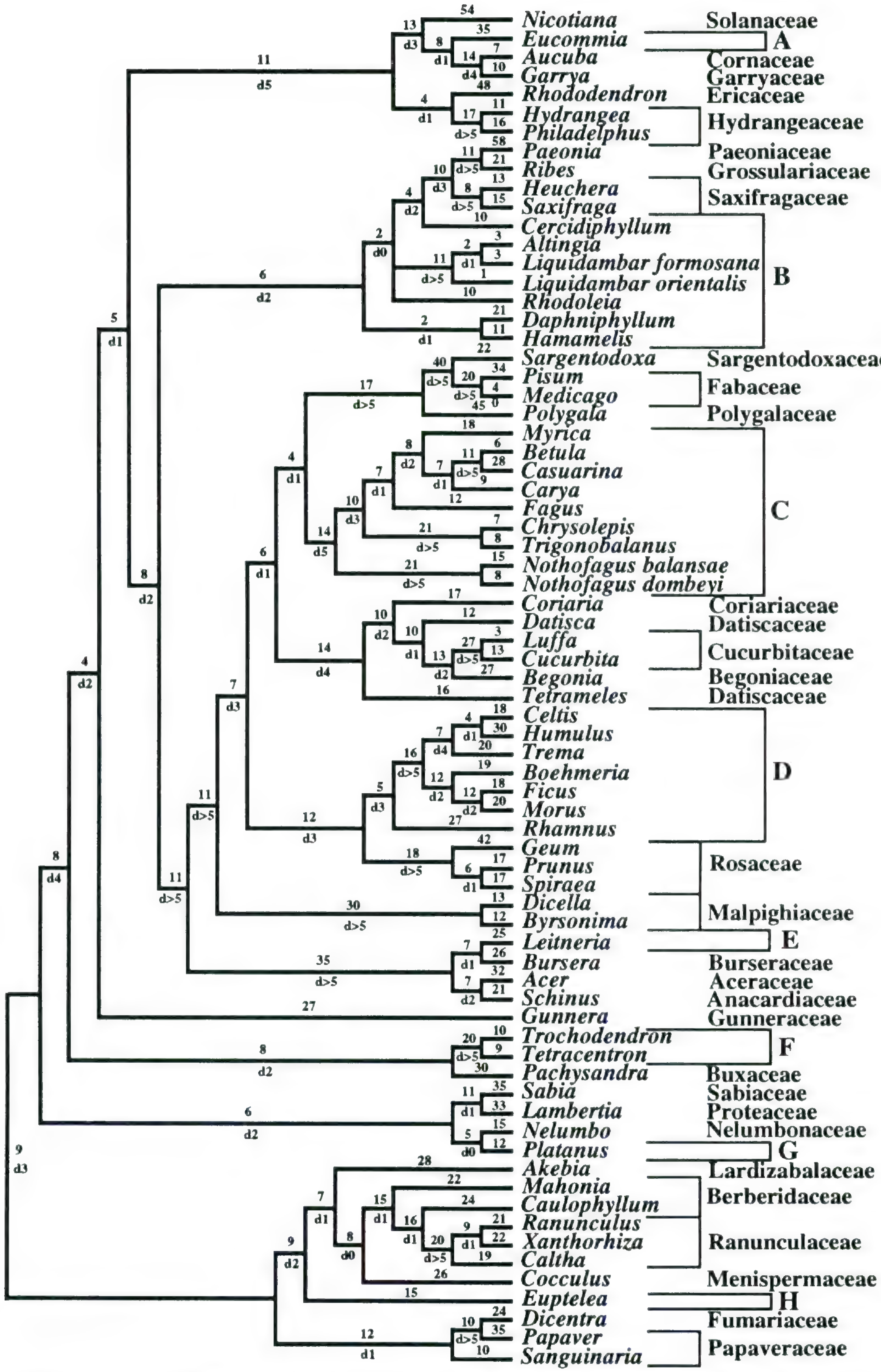



FIGURE 16. An example of using the general analysis to focus a narrower study of internal support for a polyphyletic Hamamelidae. Numbers above the horizontal lines indicate the number of substitutions optimized (ACCTRAN) onto one of the most parsimonious trees found using character-state weighting (i.e., these are Fitch steps, equal weighting). The numbers below the horizontal lines (preceded with a "d") are the number of steps less parsimonious at which a branch becomes a polytomy with the branch interior to it. Branches that are not present in the strict consensus of most-parsimonious Fitch trees are indicated by "d0," signifying that they "decay" at maximum parsimony. Groups of taxa often considered to be members of Hamamelidae are bracketed and lettered to designate putatively independent lineages (for further explanation see text).

# AN ANALYSIS OF RELATIONSHIPS WITHIN THE CUPRESSACEAE SENSU STRICTO BASED ON *rbc*L SEQUENCES[1]

*Paul A. Gadek and Christopher J. Quinn*[2]

ABSTRACT

The analysis of *rbc*L sequences of representative species of 13 of the 20 genera of the Cupressaceae sens. str. has produced a cladogram that agrees with data derived from other sources. The monophyly of the family is well supported. The cladogram provides support for the recognition of a basically northern subfamily (Cupressoideae) and a southern subfamily (Callitroideae), but the boundary between the subfamilies needs to be realigned by moving *Tetraclinis* from the Callitroideae to the Cupressoideae. The tribal arrangement of Li is largely artificial: the Libocedreae, Cupresseae, and Thujopsideae are clearly paraphyletic.

While there is evidence from morphology, leaf and wood anatomy (Eckenwalder, 1976; Hart, 1987; Quinn & Gadek, 1988), and seed proteins (Price & Lowenstein, 1989) to support the monophyly of the Cupressaceae sensu stricto, the data for some of these characters, as well as for leaf biflavonoids (Gadek & Quinn, 1983, 1985), wood anatomy (Quinn et al., unpublished), and immunological comparisons of seed proteins (Price, pers. comm.), have not correlated well with the widely accepted intrafamilial classification of Li (1953; Table 1). Cladistic analyses of the database have shown a high level of homoplasy (Gadek & Quinn, unpublished). We therefore initiated an analysis of *rbc*L sequences in representative taxa in the hope of obtaining evidence of a more conservative nature that will permit estimates of relationships within the family.

## MATERIALS AND METHODS

Species from which *rbc*L sequence data were obtained are listed in Tables 2 and 3 and are drawn from genera in both subfamilies and all six tribes (Table 1). Sequences will be lodged in Genbank on completion; they are also available from the authors.

Total DNA was isolated using the CTAB method (Doyle & Doyle, 1990). A series of synthetic oligonucleotide primers based on the *rbc*L sequences of *Nicotiana tabacum* and *Zea mays*, as well as one provided by M. W. Chase (designed by Helen Michaels and Jeff Palmer), were used for cyclic DNA amplification initially to produce a double stranded product containing the *rbc*L gene and subsequently to obtain single stranded products of both strands. The latter were sequenced by the standard dideoxy chain termination method. Sequences have been verified by sequencing both strands. The primer at the 5′ end included the first 16 bases of the gene, while that at the 3′ end was outside the coding portion of the gene. Hence, sequences start from the first complete codon (position 19) and terminate at the end of the stop codon (position 1428), a total length of 1,410 bp.

Sequences of *Glyptostrobus* and *Cryptomeria* (unpublished, Soltis et al., pers. comm.) were included as representatives of the Taxodiaceae, the generally accepted sister group for the Cupressaceae sens. str. Phylogenetic analyses were performed with PAUP version 3.0g (Swofford, 1991) using both the default character-state weightings as well as the model of Albert et al. (1993). The default weightings give equal weighting to all character states, while the Albert model invokes a tree-searching procedure that differentially weights

[1] We acknowledge the assistance of the following: W. D. Clark, Arizona State University, for advice on sequencing and analysis and help in gaining access to unpublished sequence data; D. Soltis, P. Soltis, and S. Brunsfeld, Washington State University, for access to unpublished sequences of *Glyptostrobus* and *Cryptomeria*; M. W. Chase, University of North Carolina (now at Royal Botanic Gardens, Kew, England), for 3′ primer; M. T. Clegg, University of California, Riverside, for the SE program; R. C. Crozier, Ching Crozier, and G. de Couet for assistance with techniques in the initial stages of this work; and N. Skelton and D. Crayn for technical assistance. This work is supported by Australian Research Council grant no. AD9031851.

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TABLE 1. Intrafamilial classification of Li (1953) for the Cupressaceae sensu stricto. Representative species of genera indicated by * were included in this study (see Table 2).

| Cupressaceae sensu stricto | |
|---|---|
| Subfamily Cupressoideae | Subfamily Callitroideae |
| Tribe Cupresseae | Tribe Actinostrobeae |
| *Cupressus** | *Actinostrobus* |
| *Chamaecyparis** | *Callitris** |
| *Fokeinia* | *Fitzroya* |
| Tribe Thujopsideae | Tribe Libocedreae |
| *Platycladus** | *Libocedrus** |
| *Thujopsis** | *Papuacedrus* |
| *Thuja** | *Pilgerodendron* |
| *Microbiota** | *Austrocedrus* |
| *Calocedrus** | *Diselma** |
| Tribe Junipereae | *Widdringtonia** |
| *Juniperus** | *Neocallitropsis* |
| | Tribe Tetraclineae |
| | *Tetraclinis** |

transversions over transitions within characters, and codon positions 2>1>3 among characters. Output trees from PAUP were also transferred into MacClade (Maddison & Maddison, Harvard University) and manipulated to test other topologies.

## RESULTS

The 5′ end of the sequences for several species are still incomplete, approximately 40 bases missing from the start of *Cupressus* and *Thuja*, and 30 from *Diselma*. Percentage sequence divergence was calculated, using the available homologous sequence data, for all taxon pairs (Table 2). There are quite low levels of divergence between some pairs of species: viz, *Juniperus conferta* and *Cupressus sempervirens* (0.7%), *Thuja occidentalis* and *Thujopsis dolobrata* (0.6%), *Platycladus orientalis* and *Microbiota decussata* (0.9%), and *Diselma archeri* and *Widdringtonia cedarbergensis* (0.9%). *Callitris rhomboidea* is clearly the most divergent species, showing divergences ranging from 5.1% (with *Calocedrus decurrens*) to 3.6% (with *Libocedrus bidwillii*). The levels of sequence divergence among the taxa indicate that the gene has the potential to be informative about relationships within the family.

Two trees were found by PAUP branch and bound analysis using the unweighted (default) character assumption and TBR swapping option. These trees differed only in placing *Calocedrus* either basal to, or as part of an unresolved trichotomy involving *Cupressus* + *Juniperus* and *Platycladus* + *Microbiota*. The tree with the lowest f-value is shown in Figure 1. The Cupressaceae sens. str. are monophyletic, and there are two monophyletic clades representing northern and southern genera. *Tetraclinis* appears with *Thuja* + *Thujopsis*, in a clade basal to the remaining northern genera, while *Chamaecyparis* is basal to the unresolved trichotomy referred to above. *Libocedrus* is basal to a clade containing all the remaining southern genera.

PAUP identifies in this data set 14 apomorphs that characterize Cupressaceae sens. str., of which 10 are unique synapomorphs. The clade comprising the southern genera is supported by seven unique synapomorphs (positions 459, 693, 1071, 1194, 1203, 1308, and 1363), and there are potentially three more synapomorphs at positions

TABLE 2. Pairwise comparisons of *rbc*L sequences, showing percent divergence. Northern species are listed above the horizontal line, southern below.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. *Microbiota decussata* | — | | | | | | | | | | | |
| 2. *Tetraclinis articulata* | 1.5 | — | | | | | | | | | | |
| 3. *Platycladus orientalis* | 0.9 | 1.8 | — | | | | | | | | | |
| 4. *Juniperus conferta* | 1.0 | 1.6 | 1.2 | — | | | | | | | | |
| 5. *Cupressus sempervirens* | 1.0 | 2.1 | 1.5 | 0.7 | — | | | | | | | |
| 6. *Calocedrus decurrens* | 2.0 | 2.6 | 2.2 | 1.9 | 2.1 | — | | | | | | |
| 7. *Chamaecyparis obtusa* | 1.4 | 2.2 | 1.6 | 1.3 | 1.6 | 2.3 | — | | | | | |
| 8. *Thuja occidentalis* | 1.3 | 1.7 | 1.5 | 1.2 | 1.6 | 2.0 | 1.6 | — | | | | |
| 9. *Thujopsis dolobrata* | 1.1 | 1.5 | 1.3 | 0.9 | 1.4 | 1.8 | 1.4 | 0.6 | — | | | |
| 10. *Diselma archeri* | 2.4 | 2.9 | 2.7 | 2.5 | 2.6 | 3.1 | 2.8 | 2.5 | 2.3 | — | | |
| 11. *Widdringtonia cedarbergensis* | 2.4 | 2.9 | 2.8 | 2.5 | 2.5 | 3.3 | 2.8 | 2.6 | 2.5 | 0.9 | — | |
| 12. *Callitris rhomboidea* | 4.2 | 3.9 | 4.5 | 4.5 | 4.8 | 5.1 | 4.5 | 4.1 | 4.0 | 3.6 | 3.6 | — |
| 13. *Libocedrus bidwillii* | 2.7 | 3.1 | 3.1 | 2.7 | 2.9 | 3.3 | 3.0 | 2.6 | 2.5 | 2.0 | 1.9 | 3.8 |

TABLE 3. Voucher specimens. All specimens are lodged in the John T. Waterhouse Herbarium (UNSW), University of New South Wales.

| Species | Source/voucher | Collector/locality |
|---|---|---|
| *Callitris rhomboidea* R. Br. ex L. C. Rich. | UNSW21734 | Gadek 13.ix.89, cult. |
| *Calocedrus decurrens* (Torrey) Florin | UNSW22326 | Gadek 1.iv.92, cult. |
| *Chamaecyparis obtusa* (Siebold & Zucc.) Endl. | UNSW21735 | Gadek 3.xii.91, cult. |
| *Cupressus sempervirens* L. | UNSW14297 | Debreczy & Racz x.80, Turkey; raised from seed. |
| *Diselma archeri* Hook. f. | UNSW21742 | Quinn 8.xii.91, Tasmania |
| *Juniperus conferta* Parl. | UNSW14290 | Gadek 13.viii.90, cult. |
| *Libocedrus plumosa* (D. Don) Sarg. | UNSW21741 | Quinn 6.xii.91, cult. |
| *Microbiota decussata* Komar. | Gadek s.n. | Gadek s.n. v.92, cult. |
| *Platycladus orientalis* (L.) Franco cv. 'Flagelliformis' | UNSW21737 | Gadek 3.xii.91, cult. |
| *Tetraclinis articulata* (Vahl) Mast. | UNSW21733 | Quinn 3.xii.91, cult. |
| | UNSW21730 | Fernando et al. 23.viii.91, cult. |
| *Thuja occidentalis* L. | UNSW21732 | Quinn 3.xii.91, cult. |
| *Thujopsis dolobrata* (L. f.) Siebold & Zucc. | UNSW21736 | Gadek 3.xii.91, cult. |
| *Widdringtonia cedarbergensis* Marsh | UNSW17574 | Quinn & Cunliffe 24.vi. 85, South Africa; raised from seed |

that are undetermined in a single species (33, 450, and 1227). Three additional apomorphs showing parallelisms elsewhere in the cladogram are also identified. The clade comprising the northern genera is supported by three apomorphs, of which two are unique synapomorphs (positions 237 and 339). There is only weak apomorphic support for other northern groupings within this clade, although *Juniperus* + *Cupressus* is characterized by three unique synapomorphs (168, 318, and 507) and *Microbiota* + *Platycladus* by one (1047).

The data set was then subjected to bootstrapping (PAUP, 100 replicates), and this provided strong support for the monophyly of the southern taxa (95%) and within it the grouping of *Diselma* + *Widdringtonia* (97%). The northern taxa, including *Tetraclinis*, clustered at the 75% level, and there was strong support for the clades comprising *Thuja* + *Thujopsis* (80%) and *Juniperus* + *Cupressus* (79%), while *Microbiota* clustered with *Platycladus* at the 63% level. The placement of *Tetraclinis* within this group was more equivocal: it clustered with *Microbiota* + *Platycladus* in 33% of trees and with *Thuja* + *Thujopsis* in 27%.

When the Albert et al. model of character-state weightings was invoked, PAUP heuristic analysis found three trees, all one step longer than the most parsimonious trees found using the equally weighted character option. All the Albert trees clustered *Tetraclinis* within the clade of *Microbiota* and *Platycladus*, and placed *Calocedrus* basal to *Chamaecyparis* (Fig. 2). The position of *Chamaecyparis* is determined by a single nonsynonymous 2nd codon position change, at position 284, for which there is considerable homoplasy within the cladogram.

## DISCUSSION

The molecular estimate of the phylogeny presented here gives strong support for the monophyly of the Cupressaceae sens. str. Monophyly of the family is also supported by the opposite and decussate phyllotaxis, the absence of a germination papilla and the compound nature of the sexine in the pollen (Ueno, 1959; Hart, 1987), and apparently also in the basipetal sequence of protoxylem differentiation within the leaves (Quinn & Gadek, 1988). There are further characters cited by Hart (1987) that show reversals or parallelisms.

Although the sampling of genera in this study is still quite limited, especially among the southern genera, some assessment of the support given to the present intrafamilial taxonomy (Table 1) by the sequence data is already possible. The southern genera form a strong clade but there is no support for the inclusion of the North African genus *Tetraclinis* within the mainly southern Callitroideae. The subfamily distinction (Li, 1953) was based on a single character, ovulate cone scales imbricate or valvate, which has been inconsistently scored in several genera by different authors (cf. Buchholz, 1948; Janchen, 1950) and which de Laubenfels (1965) described as "spurious." Independent ev-

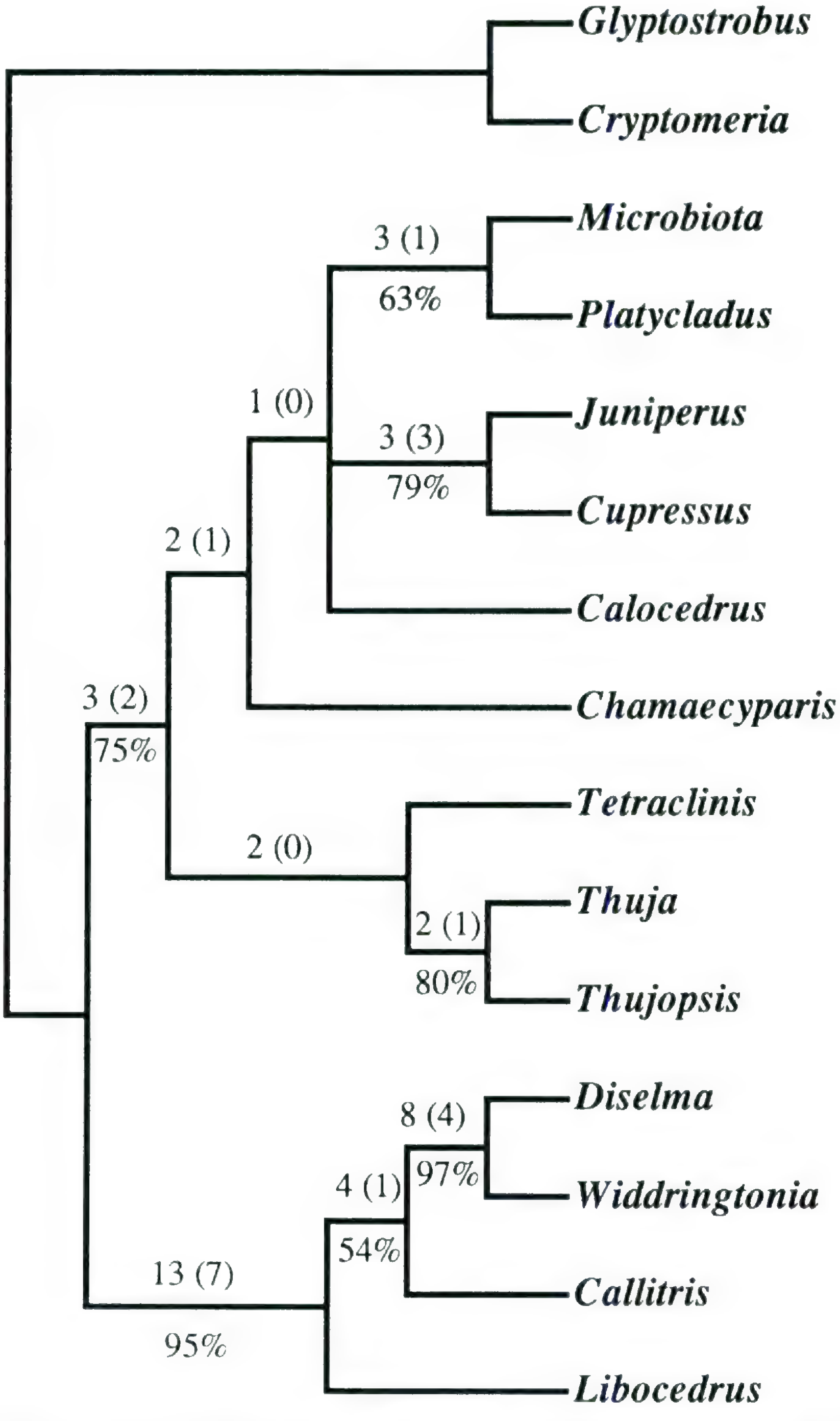


FIGURE 1. One of two shortest trees found by PAUP branch and bound analysis, arranged with *Glyptostrobus* and *Cryptomeria* (Taxodiaceae) as the outgroup. The tree shown is that with the lowest f-value. Apomorphic support as identified by PAUP is indicated above the branches, with the number of unique synapomorphs in brackets. Frequency of occurrence in bootstrap replicates of groups of taxa to the right of the branch are indicated as a percentage below the branch.

idence of an affinity between *Tetraclinis* and certain northern genera, especially *Cupressus* and *Juniperus*, has come from recent work on seed proteins (Price, pers. comm.), leaf biflavonoids (Gadek & Quinn, 1985), and transfusion tracheids (Gadek & Quinn, 1988).

The pattern of relationships within the northern and southern clades (Fig. 1) is strikingly at variance

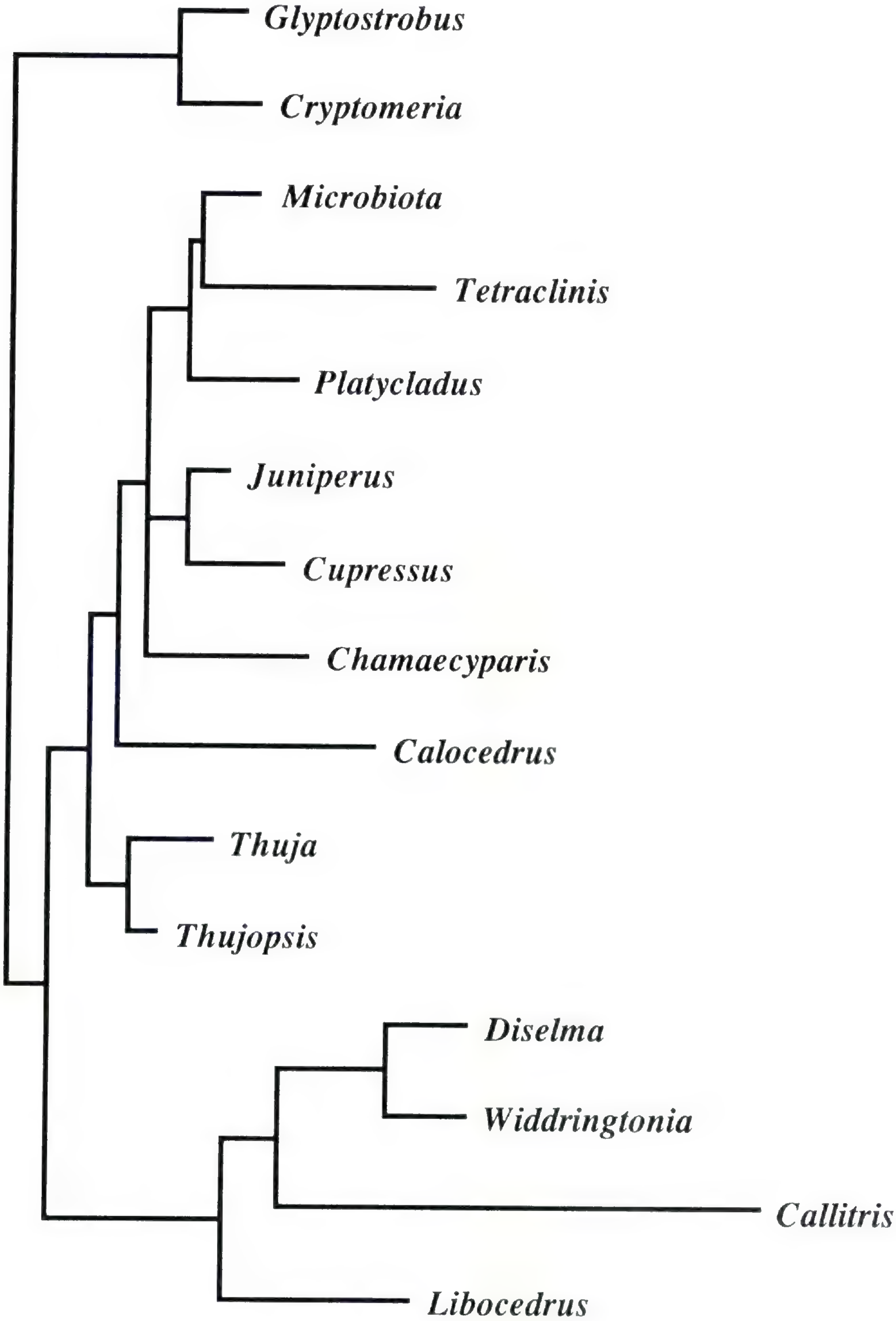


FIGURE 2. One of three shortest trees found using PAUP after invoking the character weighting assumptions of Albert et al. (1993), shown with relative branch lengths. The other two trees resolve the trichotomy by placing *Chamaecyparis* either basal to the other two clades, or basal within the *Juniperus–Cupressus* clade. In each case, PAUP assigns a relative branch length of zero to these internodes. The tree shown is one step longer than that in Figure 1.

with the tribal groups of Li (1953). The placement of *Callitris* (Actinostrobeae) as sister group to *Diselma* + *Widdringtonia* (Libocedreae) renders the latter tribe paraphyletic. The monophyly of neither the Cupresseae (*Cupressus* and *Chamaecyparis*) nor the Thujopsideae (*Thuja*, *Thujopsis*, *Calocedrus*, *Platycladus*, and *Microbiota*) is supported by the sequence data. Indeed, all the trees derived from PAUP using either default or Albert et al. character-state weightings, and from the bootstrap analysis, contain the same three strong clades within the northern genera: *Juniperus* + *Cupressus*, *Microbiota* + *Platycladus*, and *Thuja* + *Thujopsis*. The position of the other northern genera is equivocal on these sequence data, but there is some evidence from the Albert trees, and the bootstrap analysis, for the association of *Tetraclinis* with the first two of these clades. Such an affinity is supported by both chemical and anatomical data: *Tetraclinis* possesses the same leaf biflavonoid pattern that distinguishes *Cupressus* and *Juniperus* (mainly parental biflavonoids with cupressuflavone a major constituent) and all five genera accumulate cupressuflavone (Gadek & Quinn, 1985; unpublished). Cupressuflavone derivatives also occur in *Calocedrus decurrens*, but are not found in the species of *Chamaecyparis* or *Thujopsis* sampled here. *Tetraclinis*, *Platycladus*, *Cupressus*, and *Juniperus* all possess trabeculate pitting in their transfusion tracheids, a state not found in *Chamaecyparis*, *Thuja*, or *Thujopsis*, while the intermediate state of barred pits occurs in *Calocedrus* (Gadek & Quinn, 1988). These same characters support the grouping of *Cupressus* with *Juniperus*, which Li (1953) assigned to a separate tribe (Table 1), rather than with *Chamaecyparis* to form the Cupresseae. They also support the separation of *Platycladus* from the *Thuja* + *Thujopsis* clade with which it has long been associated. The close association of *Thuja* and *Thujopsis* accords with other available data, and their divergence from the other northern genera finds some support from wood characters (Hart, 1987). The lack of a robust resolution of affinities between these clades and other northern genera, however, particularly with regard to the placement of *Chamaecyparis*, *Calocedrus*, and *Tetraclinis*, is a reflection of the low evolutionary rate of divergence of the *rbc*L gene within this group. Sequence data from a faster-evolving gene may help resolve the cladogram.

## Conclusions

The analysis of *rbc*L sequences of representative species of 13 of the 20 genera of the Cupressaceae sens. str. has produced a cladogram that finds considerable support from data derived from other sources. The monophyly of the family is well supported. The cladogram provides support for the recognition of a basically northern subfamily (Cupressoideae) and a southern subfamily (Callitroideae), but the boundary between these subfamilies needs to be realigned by moving *Tetraclinis* from the Callitroideae to the Cupressoideae. The tribal arrangement of Li (1953) is largely artificial: the Libocedreae, Cupresseae, and Thujopsideae are clearly paraphyletic. Although some robust clades are recognized (viz, *Diselma* + *Widdringtonia*, *Juniperus* + *Cupressus*, and *Thuja* + *Thujopsis*), the present database will not provide a robust resolution of relationships among the genera because of the low evolutionary rate of divergence of the *rbc*L sequences, especially within the northern subfamily.

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# MOLECULAR PHYLOGENETICS OF THE MAGNOLIIDAE: CLADISTIC ANALYSES OF NUCLEOTIDE SEQUENCES OF THE PLASTID GENE *rbc*L[1]

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## Abstract

Nucleotide sequences of the plastid protein-coding gene *rbc*L from 64 species of 36 families in subclass Magnoliidae sensu Cronquist and representatives of all other major seed plant groups were analyzed by parsimony in a series of four analyses. *Ceratophyllum* (Ceratophyllaceae) was found to be sister to all other angiosperms. Other magnoliids formed five major groups, roughly corresponding to the Magnoliales, Laurales, Aristolochiaceae/Piperales, Nymphaeales, and Ranunculales/Papaverales. Four magnoliid lineages, those with monosulcate or monosulcate-derived pollen (Magnoliales, Laurales, Aristolochiales/Piperales, and Nymphaeales), and the monocots (with the same type of pollen) formed a weakly supported monophyletic group. The Illiciales (Illiciaceae and Schisandraceae), with a unique type of tricolpate pollen, also fell into this monosulcate clade. Relationships among these major lineages were resolved in all trees, but with low levels of support. Magnoliidae with tricolpate and tricolpate-derived pollen, Ranunculales Papaverales and Nelumbonaceae, fell into the other large clade of angiosperms, which have sometimes been termed the eudicots. Monophyly of this large tricolpate clade was strongly supported. These results demonstrated a high degree of congruence with the major groups identified in other studies, but they differed in the general relationships of these groups, particularly the monophyly of the monosulcate taxa and the sister-group relationship of angiosperms with the two general pollen types. They also deviated in the specific taxon composition of some major clades.

The dicotyledonous subclass Magnoliidae (Cronquist, 1981) contains most of the putatively primitive angiosperms. A thorough phylogenetic understanding of the complex is critical for study of the origin and reconstruction of the phylogeny of angiosperms. The Euanthial Theory of angiosperm evolution (Arber & Parkin, 1907) postulates that angiosperms with large strobiloid flowers such as Magnoliales are more primitive than those with diminutive, simple flowers (e.g., Piperales and Chloranthaceae). Over the past two decades, however, paleobotanists have accumulated a large body of fossil evidence which suggests that, during their early evolution, angiosperms with small and simple flowers might have paralleled or preceded those with large and complex flowers (Dilcher, 1979; Upchurch, 1984; Crane et al., 1986; Friis et al., 1986; Crane, 1989; Taylor & Hickey, 1990; Pedersen et al., 1991). A similar challenge has come from studies of extant plants (Burger, 1977, 1981; Hamby & Zimmer, 1992; Taylor & Hickey, 1992). Furthermore, which particular groups of Magnoliidae are related to the monocots and eudicots (the dicots with tricolpate and tricolpate-derived pollen

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types, exclusive of Illiciales, cf. Walker & Doyle, 1975; Doyle & Hotton, 1991) remains a debatable issue (Dahlgren & Clifford, 1982; Dahlgren et al., 1985; Walker & Walker, 1984; Donoghue & Doyle, 1989; Doyle & Hotton, 1991).

The Magnoliidae have been known as the ranalian complex, Ranales, or Polycarpicae. In the classification scheme of A. P. de Candolle (1824), their prototype first appeared; it included key families of Magnoliales (Magnoliaceae, with *Illicium* of Illiciaceae and *Drimys* and *Tasmannia* of Winteraceae; and Annonaceae, with *Kadsura* of Schisandraceae), Nymphaeales (Nymphaeaceae, with *Nelumbo* of Nelumbonaceae), and Ranunculales/Papaverales (Ranunculaceae; Menispermaceae, with *Lardizabala* of Lardizabalaceae; Berberidaceae; Papaveraceae; and Fumariaceae). These taxa were placed sequentially at the beginning of the system, which covered only dicots and gymnosperms, but no collective name was given to this aggregation of families. Lindley (1833) was the first one to erect two taxa, Ranales and Anonales, to cover this group of plants. In *Genera Plantarum*, Bentham & Hooker (1862) followed de Candolle's treatment for this complex, except for addition of a lauralean family, the Calycanthaceae; they placed all these taxa together under Ranales. Situating these families at the beginning of the classification systems antedated formulation of the Euanthial Theory by Arber & Parkin (1907), which equated flowers of the Magnoliales to Bennettitalean strobili and provided a theoretical explanation for recognizing Magnoliidae as the primitive angiosperms. Eichler (1890) and Engler & Prantl (1891), despite advocating Amentiferae as the primitive angiosperms, also made a significant contribution to development of the ranalian concept by adding to the complex the major lauralean families, Hernandiaceae, Lauraceae, and Monimiaceae, and several other taxa such as Lactoridaceae and Trochodendraceae (also including *Cercidiphyllum* of Cercidiphyllaceae and *Eupteleа* of Eupteleaceae). In his 1915 paper, often regarded as the first truly phylogenetic classification, Bessey brought to the ranalian complex the piperalean families (Piperaceae, Saururaceae, and Chloranthaceae). By early this century, the Magnoliidae were conceptually mature and comprised five major lineages: Magnoliales, Laurales, Piperales, Nymphaeales, and Ranunculales/Papaverales.

Modern systematists (Takhtajan, 1987; Cronquist, 1988; Dahlgren, 1989; Thorne, 1992) have agreed upon the basal position of Magnoliidae in angiosperms and recognition of the five major lineages; nonetheless, their opinions differ widely on relationships among these lineages. Takhtajan (1987) divided the complex into two subclasses, placing monosulcate lineages in Magnoliidae and tricolpate lineages in Ranunculidae (but Illiciales and Nelumbonaceae were in the former). Dahlgren's (1989) treatment of the complex resembled that of Takhtajan (1987), but no higher categories were given to the two assemblages, Magnolianae/Nymphaeanae and Ranunculanae (cf. fig. 1 in Dahlgren, 1989). In the monosulcate assemblage, Dahlgren placed Piperales with Nymphaeales, rather than with Magnoliales and Laurales as in Takhtajan's (1987) scheme. A major difference between Cronquist's (1981, 1988) and Takhtajan's (1980, 1987) systems is that Cronquist did not recognize Ranunculales/Papaverales as a separate subclass. Thorne (1992) divided the complex into three superorders, Annonanae (including most monosulcate families plus Ranunculales/Papaverales), Nymphaeanae, and Rafflesianae (the latter two narrowly defined).

Relationships of several isolated families, Austrobaileyaceae, Ceratophyllaceae, Chloranthaceae, Illiciaceae/Schisandraceae, Lactoridaceae, and Nelumbonaceae, have been extensively debated. These taxa are either included in one of the major lineages of Magnoliidae or treated as independent minor groups, but their affinities are typically stated to be uncertain.

Recently, several cladistic studies of morphological, phytochemical, and molecular data have attempted to answer some of the questions concerning the phylogenetics of Magnoliidae (Dahlgren & Bremer, 1985; Donoghue & Doyle, 1989; Loconte & Stevenson, 1991; Martin & Dowd, 1991; Hamby & Zimmer, 1992; Taylor & Hickey, 1992). These efforts have met with only partial success due to: (i) widespread homoplasy in primitive angiosperms, (ii) problems of choosing appropriate ingroups and outgroups, (iii) difficulty of coding characters in morphological cladistic studies, or (iv) insufficient sampling (a major problem in the molecular investigations).

Protein-coding genes have been shown to reflect the genealogical history of organisms (Atchley & Fitch, 1991), though to what degree and at what taxonomic level this is true awaits further study. Evolutionarily conservative genes, such as *rbc*L, which codes for the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), are considered suitable for study of relationships among taxa of higher rank (Ritland & Clegg, 1987; Zurawski & Clegg, 1987; Palmer et al., 1988). They provide new characters that permit an in-

dependent evaluation of phylogenetic relationships among plant groups uninfluenced by previous ideas of transformation of morphological characters and putative relationships among taxa. In the present study, we perform parsimony analyses of *rbc*L sequences from species representing almost all magnoliid families and endeavor to (1) evaluate the concepts of Magnoliidae, (2) identify major lineages in the subclass, investigate relationships within these major lineages, and assess affinities of several problematic taxa, (3) determine the relative phylogenetic positions of the major lineages within Magnoliidae, and (4) examine relationships of the Magnoliidae to monocots and eudicots.

## Material and Methods

Well aware of the pitfalls caused by inadequate sampling of sequence variation (Albert et al., 1993; Chase et al., 1993), we sampled at least one species from each family (this of course does not address adequately the putative monophyly of these families). Thus 64 species from 36 families representing all orders of the Magnoliidae were included (we follow the classification scheme of Cronquist, 1981, unless otherwise indicated). These taxa are listed in the Appendix at the end of this issue. Several sequences have been published previously (Golenberg et al., 1990; Les et al., 1991). Missing families are Circaeasteraceae, Gomortegaceae, Trimeniaceae, Hydnoraceae, and Rafflesiaceae (Takhtajan, 1987; Dahlgren, 1989; Thorne, 1992). It is likely that the last two, which are achlorophyllous, lack *rbc*L, as was found in other parasitic plants (dePamphilis & Palmer, 1990).

Total cellular DNA was extracted using the modified CTAB method (Doyle & Doyle, 1987) from 0.6–2.0 g fresh or silica gel-dried leaves (Chase & Hills, 1991) collected from a single plant (in the case of *Hernandia ovigera* L., the leaf was removed from a 22-year-old herbarium specimen). All DNAs were purified by CsCl-ethidium bromide gradient centrifugation. A fragment containing the gene *rbc*L was amplified using a thermo-stable DNA polymerase and two synthetic 26-mer primers based on the *rbc*L sequences from *Zea mays* L. and *Nicotiana tabacum* L. The amplified fragment was ligated into Bluescript vector and cloned with standard recombinant techniques. Sequencing was performed using Sequenase 2.0 (US Biochemical, Inc.) for dideoxynucleotide chain-termination reactions, and sequences were obtained from both strands. For several species, the gene was directly sequenced from the amplified fragment without cloning.

Sequence data were analyzed using PAUP 3.0s (Swofford, 1991). Several searches were conducted to approach problems at different scales and with different techniques.

**Search A.** All 65 magnoliid sequences were analyzed together with 434 other seed plant *rbc*L sequences (see Chase et al., 1993) to identify major lineages in the Magnoliidae, determine relative position of these lineages, and examine relationships of the subclass to monocots and eudicots. Two sequences of *Canella winterana* (L.) Gaertner, both with intact reading frames, were obtained from the DNA sample extracted from a single plant. They differ by 57 base pairs; 24, 15, and 18 of these differences occur at the first-, second-, and third-codon position, respectively. Both sequences were used in all analyses; one of them may be a "pseudogene." Due to the magnitude of the data set and the limitation of the software, the level of parsimony of this broad search was not certain (see Chase et al., 1993, for a more detailed explanation and discussion of the result of this larger analysis). This search helped us select a smaller number of taxa for a "manageable" analysis to examine internal support.

**Search B.** We performed another analysis with all monosulcate magnoliid sequences plus selected gymnosperms, monocots, and eudicots that served as place-holders for their respective groups identified in Search A. An analysis under the Fitch criterion (equal weights for all substitutions; Fitch, 1971) using 2,000 random sequence additions, STEEPEST DESCENT, MULPARS (but permitting only 10 trees to be held at each step), and NNI (nearest-neighbor interchange) found only one island of trees. All trees within this island were recovered by using the trees found in the random searches as starting points with MULPARS and TBR (tree bisection-reconnection) until swapping was completed.

**Search C.** To examine the effect of distant outgroups such as Gnetales on the ingroup network, we conducted an ingroup-only analysis of flowering plants. Again, this analysis was performed under the Fitch criterion using 2,000 random sequence additions in the same manner as described above. In addition to the same set of monosulcate magnoliids and monocots as were used in Search B, representative species of all families in the Ranunculales/Papaverales were included to investigate interfamilial relationships within this group. Two islands of equally parsimonious trees were found, and all of the trees in each of those islands were recovered by the same method as in Search B (swapping to completion with MULPARS and TBR).

To gain a measure of the robustness of the topology, decay of parsimony (Bremer, 1988) was examined. All maximum parsimony trees of both islands were used as starting trees to search for trees up to five steps less parsimonious; the FILTER TREES option was used to identify trees at each length, and a strict consensus tree was computed at each step. The number of steps less parsimonious at which a branch collapsed was recorded as the decay index. The larger the number, the more robust a branch. A decay index of 1 indicates that the branch is present in all maximum parsimony trees but collapses at maximum parsimony plus one step.

**Search D.** There has been great interest in recent cladistic studies to determine the basalmost lineage of angiosperms. The Nymphaeales are often claimed as a sister group to all other angiosperms (Donoghue & Doyle, 1989; Hamby & Zimmer, 1992), but our results did not place them in such a position. To evaluate the hypothesis of Nymphaeles being the basalmost angiosperms, we performed a topology constraint experiment using the same set of taxa as in Search B, but with the Nymphaeales constrained to be sister to all other angiosperms (using the CONSTRAINTS option of PAUP). The search was conducted under the Fitch criterion using 2,000 random sequence additions in the same manner as described in Search B. This is a more accurate means to determine the loss of parsimony associated with an alternate topology; merely constraining the topology based on the shortest trees found overall without performing branch swapping is likely to result in an inaccurate assessment of tree length because it does not permit character transformations to be optimized on different branches than in the unconstrained trees.

## Results

**Search A.** A strict consensus tree was computed from 3,900 equally parsimonious trees at a length of 16,305 steps (Chase et al., 1993). These trees have a consistency index (C.I.; for potentially synapomorphous characters) of 0.102 and a retention index (R.I.) of 0.638; a summary of this tree is shown in Figure 1 (for the detailed version of the strict consensus tree, see Chase et al., 1993). Exclusive of *Ceratophyllum*, which is sister to all other flowering plants, the angiosperms are split into two clades that correspond to the two general pollen types, monosulcate and tricolpate (for the sake of convenience, we refer to angiosperms with monosulcate and monosulcate-derived pollen types as the "monosulcates" and those with tricolpate and tricolpate-derived pollen types as the "eudicots," the latter in accord with Doyle & Hotton's, 1991, use of that term). Five major lineages are identified among the Magnoliidae; they are roughly equal to the Magnoliales, Laurales, Piperales (including Aristolochiaceae and Lactoridaceae), Nymphaeales (excluding Nelumbonaceae but including Amborellaceae, Austrobaileyaceae, Chloranthaceae, and Illiciales), and Ranunculales (excluding Coriariaceae, Sargentodoxaceae, and Sabiaceae but including Eupteleaceae, Fumariaceae, and Papaveraceae). (We will use these ordinal circumscriptions throughout the rest of this paper; i.e., under Piperales we will include Aristolochiaceae and Lactoridaceae, unless stated otherwise.) The four magnoliid lineages with monosulcate pollen types, (i) Magnoliales, (ii) Laurales, (iii) Piperales, and (iv) Nymphaeales, plus the monocots (with the same type of pollen), form a clade. The Illiciales, which have anomalous tricolpate pollen (see below), also fall into this monosulcate clade. The Piperales are sister to all other monosulcates; Magnoliales/Nymphaeales, Laurales, and monocots form an unresolved trichotomy in the strict consensus tree. The Ranunculales, Nelumbonaceae, and Sabiaceae, all of which have tricolpate pollen, together with other angiosperms possessing the same pollen type, form a monophyletic group. This large clade corresponds to Walker & Doyle's (1975) nonmagnoliid dicots or Doyle & Hotton's (1991) "eudicots." The Ranunculales are sister to the rest of the eudicots. In another basal lineage of eudicots are Nelumbonaceae and Sabiaceae (with Platanaceae and Proteaceae; hamamelid I, Fig. 1). The Coriariaceae and Sargentodoxaceae are not affiliated with the Magnoliidae, the former being sister to the clade of Cucurbitaceae/Begoniaceae/Datiscaceae and the latter imbedded in the Fabaceae (both in rosid I, Fig. 1; also see fig. 11B in Chase et al., 1993).

**Search B.** A single island of 46 trees at a length of 3,414 steps with C.I. of 0.275 (unique substitutions excluded) and R.I. of 0.566 was found. One of these maximum parsimony trees favored by the weighting criterion (Albert et al., 1993) is shown with Fitch branch lengths optimized on it (ACCTRAN optimization; Fig. 2). Even though far fewer taxa (82 species) were used in Search B, the same general topology as Search A was obtained.

**Search C.** Two islands of 89 and 3 trees respectively, at a length of 2,674 steps with C.I. of 0.346 (unique substitutions excluded) and R.I. of 0.531 were found. For illustration, one tree from each island was selected using the weighting criterion of Albert et al. (1993). The trees in the

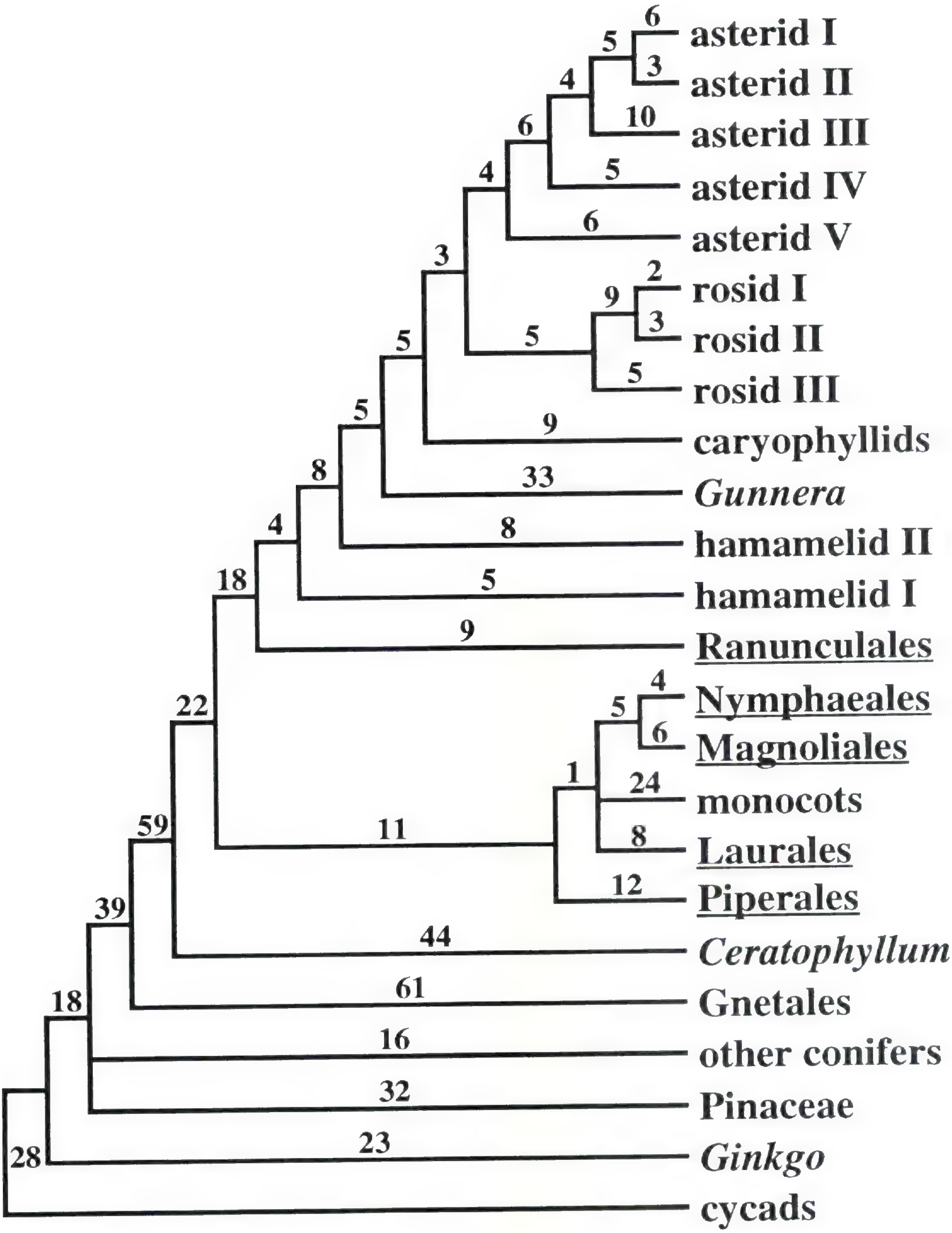
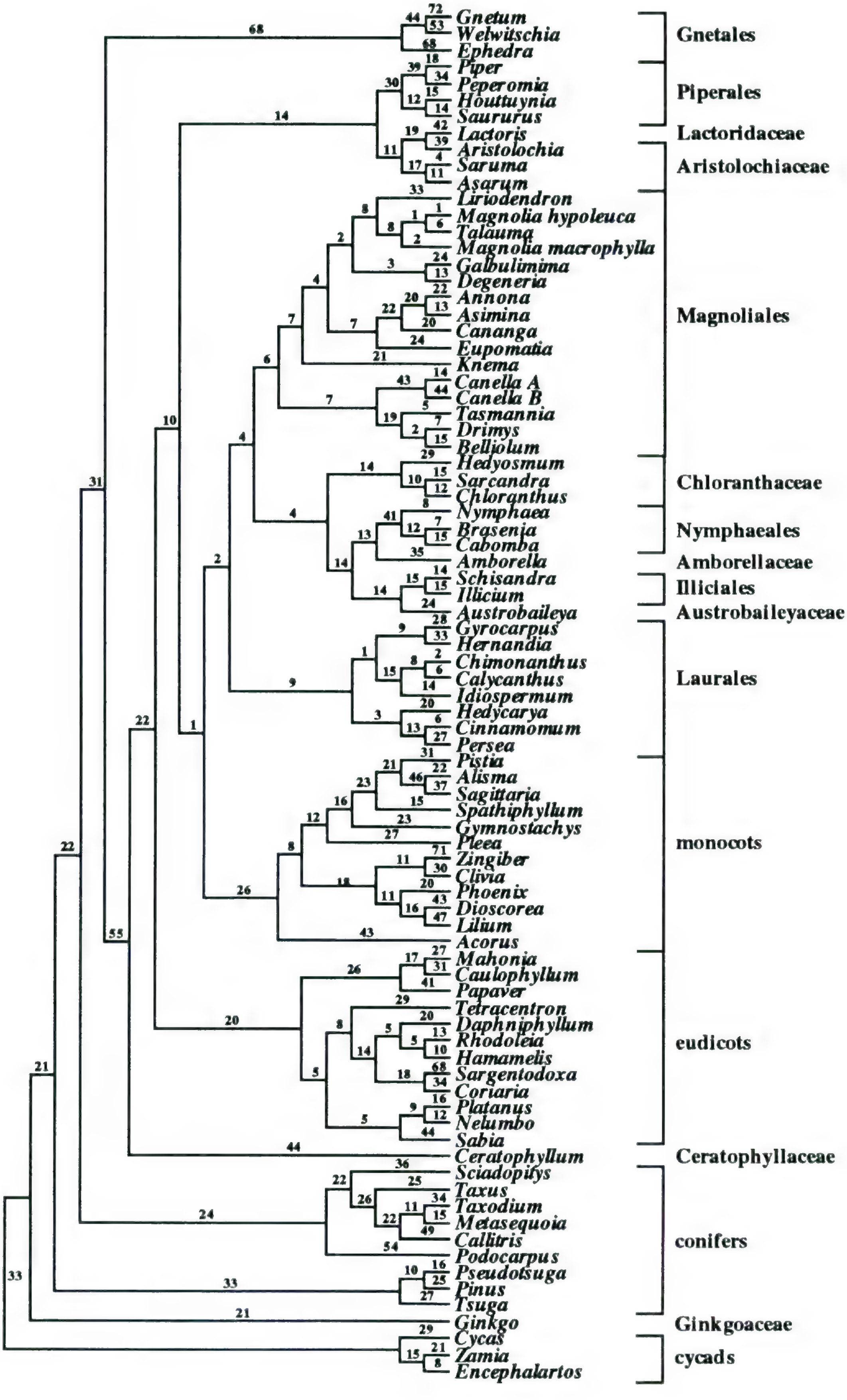



FIGURE 1. Summary of the strict consensus tree of 3,900 equally parsimonious trees at a length of 16,305 for *rbc*L sequences from 499 species of seed plants using Fitch (1971) parsimony (branch lengths are from one of the trees). The ingroup network is arranged with the cycads sister to all other seed plants. The five major lineages of the Magnoliidae identified are underlined. Nelumbonaceae and Sabiaceae are in hamamelidae I; Coriariaceae and Sargentodoxaceae are in rosid I. For a detailed explanation of the composition of all clades in this figure, see Chase et al. (1993).


Gnetum
Welwitschia
Ephedra
Piper
Peperomia
Houttuynia
Saururus
Lactoris
Aristolochia
Saruma
Asarum
Liriodendron
Magnolia hypoleuca
Talauma
Magnolia macrophylla
Galbulimima
Degeneria
Annona
Asimina
Cananga
Eupomatia
Knema
Canella A
Canella B
Tasmannia
Drimys
Belliolum
Hedyosmum
Sarcandra
Chloranthus
Nymphaea
Brasenia
Cabomba
Amborella
Schisandra
Illicium
Austrobaileya
Gyrocarpus
Hernandia
Chimonanthus
Calycanthus
Idiospermum
Hedycarya
Cinnamomum
Persea
Pistia
Alisma
Sagittaria
Spathiphyllum
Gymnostachys
Pleea
Zingiber
Clivia
Phoenix
Dioscorea
Lilium
Acorus
Mahonia
Caulophyllum
Papaver
Tetracentron
Daphniphyllum
Rhodoleia
Hamamelis
Sargentodoxa
Coriaria
Platanus
Nelumbo
Sabia
Ceratophyllum
Sciadopitys
Taxus
Taxodium
Metasequoia
Callitris
Podocarpus
Pseudotsuga
Pinus
Tsuga
Ginkgo
Cycas
Zamia
Encephalartos
Gnetales
Piperales
Lactoridaceae
Aristolochiaceae
Magnoliales
Chloranthaceae
Nymphaeales
Amborellaceae
Illiciales
Austrobaileyaceae
Laurales
monocots
eudicots
Ceratophyllaceae
conifers
Ginkgoaceae
cycads

larger island (Fig. 3), though less resolved, are congruent in the general topology with the trees from Search B (Fig. 2). In contrast, the trees of the smaller island (Fig. 4) are different from those found in Search B; *Ceratophyllum* allies with *Canella* in the Magnoliales rather than being situated in an isolated position. These trees were arranged to agree with the results of two previous searches (i.e., with the eudicots sister to the monosulcates).

Many parts of this topology (Fig. 3) do not demonstrate strong internal support (decaying at two or fewer steps less parsimonious). At the level of the relationships among the major groups identified, all are weakly supported (even though the monophyly of some of the orders themselves are strongly supported; see below). The shift of *Ceratophyllum*, which is the only taxon with a different position in the two islands of trees, demonstrates its low level of internal support. It would appear that the use of distant outgroups such as Gnetales may be introducing homoplasy such that the smaller island does not exist at maximum parsimony in Search B (we cannot evaluate the degree of parsimony of the trees or the existence of other islands of equally parsimonious trees in Search A because of the size of the data set). Groups with moderate to strong support (decaying at three or more steps less parsimonious; Fig. 3) are eudicots, monocots, Laurales, "core" Magnoliales (excluding Canellaceae and Winteraceae), Nymphaeales (including the associated woody families, but excluding Chloranthaceae), Piperales, and Ranunculales.

**Search D.** A single island of 186 trees at a length of 3,425 steps with C.I. of 0.274 (unique substitutions excluded) and R.I. of 0.565 was found. One of the maximum parsimony trees chosen by the weighting criterion is shown in Figure 5. Compared with the trees from Search B (length of 3,414 steps; the same taxa are present in both), the trees recovered in this search are only slightly less parsimonious: 11 steps or only 0.32% longer.

Although relationships among the four monosulcate magnoliid lineages, monocots, and eudicots are resolved with only low levels of support, these clades are consistently identified, and relationships within the clades remain unchanged in the series of analyses (Figs. 1, 2, 3, 4). Even though the constraint experiment makes the group related to the Nymphaeales paraphyletic to all other angiosperms, it leaves them in near proximity to each other and otherwise identifies the same major lineages as in the previous searches. *Ceratophyllum* is the single taxon that shifts wildly with each treatment.

## Discussion

### 1. Phylogenetic evaluation of the Magnoliidae

From the review of historical development of the ranalian concept and the treatment of the complex in several modern classification systems presented in the introduction, it is clear that five major lineages, Magnoliales, Laurales, Piperales, Nymphaeales, and Ranunculales, were consistently recognized. In this study, we obtained clades that are roughly equal to these traditionally recognized lineages, and they occupy basal positions among angiosperms. Our analyses were conducted only under the criterion of parsimony, and we did not rely on any previous hypothesis concerning evolution of morphological characters or putative relationships among these taxa. The high degree of correspondence between the clades identified in this study and those traditionally recognized categories provides support for these lineages (even though support for several of these was weak in our study) and is an indication that *both* morphology and *rbc*L sequences are informative for phylogenetic reconstruction.

The split of the angiosperms, exclusive of *Ceratophyllum*, into a monosulcate and eudicot clade in our results was unexpected. Monophyly of the monosulcates has never been suggested, and at present we know of no unequivocal morphological or phytochemical characters to define the clade. Possession of monosulcate pollen is not a synapomorphy because this pollen type is also found in nonflowering seed plants. The ethereal oil cells could be a potential synapomorphy for the monosulcates; they occur in all component lineages (at least in some basal members) of this clade and absence of these cells in Amborellaceae/Nymphaeales and most monocots (basal monocots such as *Acorus* have the ethereal oil cells, Cronquist, 1981) can be interpreted as due to secondary loss. A close relationship between the Magnoliidae and the monocots has been proposed by Huber (1977), Hegnauer (1977), and Kubitzki & Gottlieb (1984),

←

Figure 2. One of the 46 maximum-parsimony (Fitch) trees from the single island found for *rbc*L sequences of 82 species of gymnosperms, monosulcate magnoliids, monocots, and eudicots. This particular tree was selected by the weighting criterion of Albert et al. (1993), but branch lengths are Fitch optimizations (ACCTRAN).

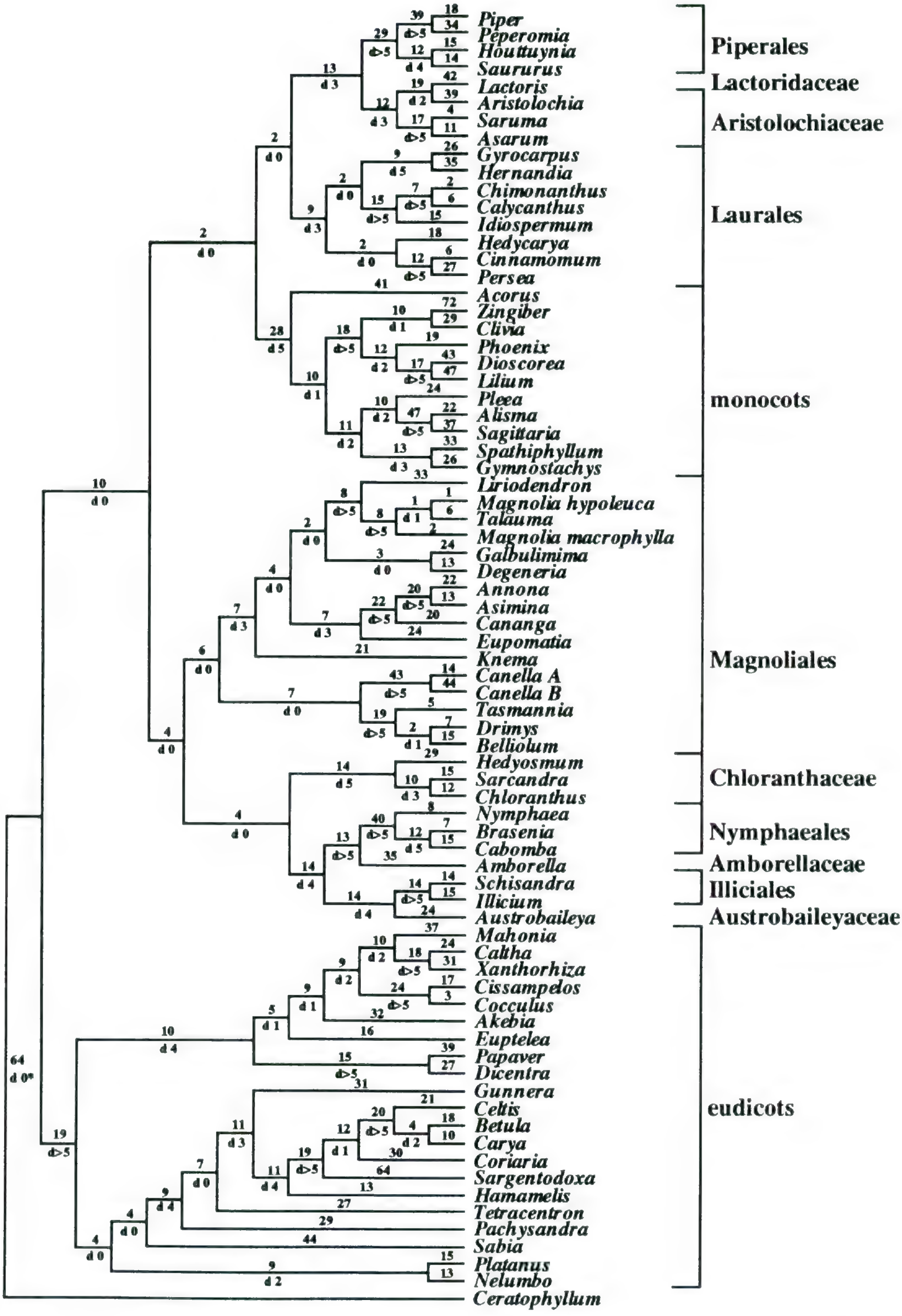



FIGURE 3. One of the 89 maximum-parsimony (Fitch) trees, chosen with the weighting criterion, from the larger of the two islands found for *rbc*L sequences of 74 species of angiosperms. The branch lengths are Fitch optimizations (ACCTRAN). Decay indices are indicated below each branch and are preceeded with a "d" ("d0" indicates a branch present in the particular tree favored by the weighting criterion but not in all maximum-parsimony trees).

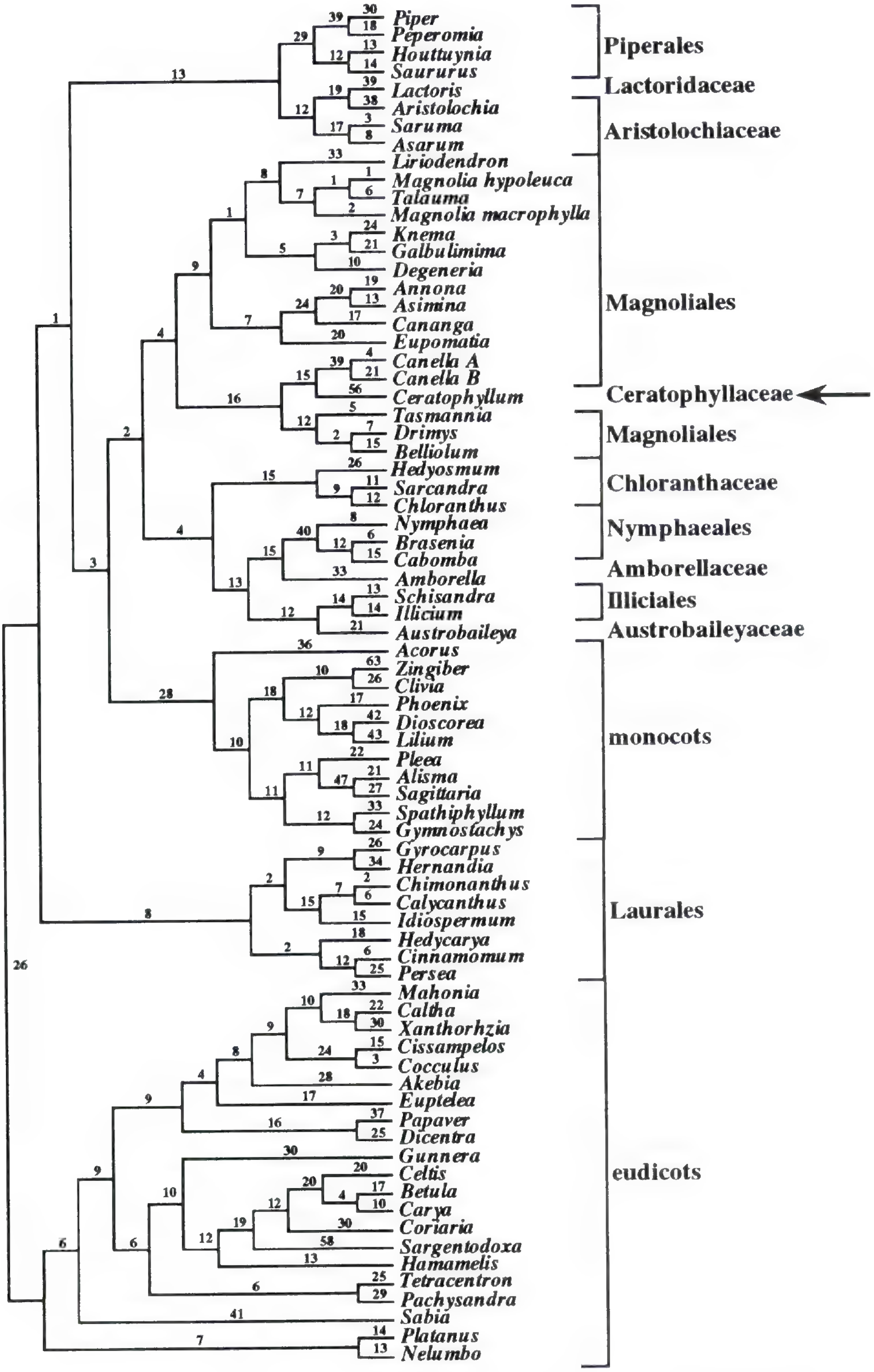
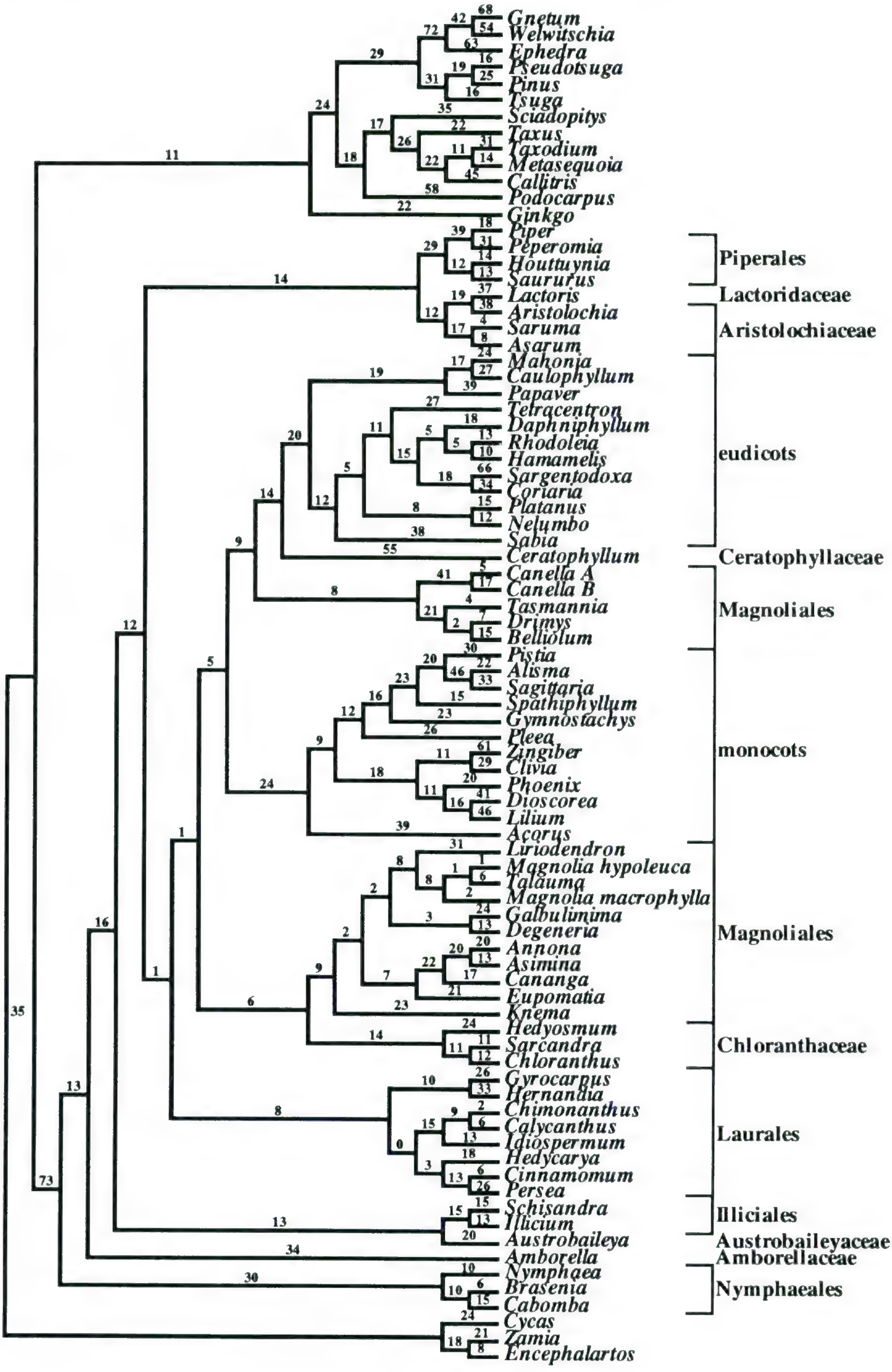



FIGURE 4. One of the three maximum-parsimony (Fitch) trees, chosen with the weighting criterion, from the smaller of the two islands found for *rbc*L sequences of 74 species of angiosperms. The branch lengths are Fitch optimizations (ACCTRAN).


Gnetum
Welwitschia
Ephedra
Pseudotsuga
Pinus
Tsuga
Sciadopitys
Taxus
Taxodium
Metasequoia
Callitris
Podocarpus
Ginkgo
Piper
Peperomia
Houttuynia
Saururus
Lactoris
Aristolochia
Saruma
Asarum
Mahonia
Caulophyllum
Papaver
Tetracentron
Daphniphyllum
Rhodoleia
Hamamelis
Sargentodoxa
Coriaria
Platanus
Nelumbo
Sabia
Ceratophyllum
Canella A
Canella B
Tasmannia
Drimys
Belliolum
Pistia
Alisma
Sagittaria
Spathiphyllum
Gymnostachys
Pleea
Zingiber
Clivia
Phoenix
Dioscorea
Lilium
Acorus
Liriodendron
Magnolia hypoleuca
Talauma
Magnolia macrophylla
Galbulimima
Degeneria
Annona
Asimina
Cananga
Eupomatia
Knema
Hedyosmum
Sarcandra
Chloranthus
Gyrocarpus
Hernandia
Chimonanthus
Calycanthus
Idiospermum
Hedycarya
Cinnamomum
Persea
Schisandra
Illicium
Austrobaileya
Amborella
Nymphaea
Brasenia
Cabomba
Cycas
Zamia
Encephalartos
Piperales
Lactoridaceae
Aristolochiaceae
eudicots
Ceratophyllaceae
Magnoliales
monocots
Magnoliales
Chloranthaceae
Laurales
Illiciales
Austrobaileyaceae
Amborellaceae
Nymphaeales

but they relied on what are probably symplesiomorphic features. Currently available fossil evidence indicates that monosulcate angiosperms antedate eudicots (Doyle, 1969; Muller, 1970, 1981, 1984; Doyle & Hickey, 1976; Hickey & Doyle, 1977; Friis & Crepet, 1987; Hughes & McDougall, 1990; Doyle & Hotton, 1991), and it has been postulated that the latter were derived from the former (Walker & Walker, 1984). Crane & Lidgard (1990), after examining palynological diversity in the Cretaceous, suggested that the monosulcates probably represent an evolutionary grade rather than a clade. Three different scenarios may explain the discrepancy between our results and these previous hypotheses. First, the fossil evidence is most certainly incomplete, and future paleobotanical exploration may find older evidence for eudicots. Second, the weakly supported monosulcate clade is perhaps generated spuriously by high levels of sequence divergence among the monosulcates, eudicots, and gymnosperms (i.e., the monophyletic monosulcate clade is the result of "long branch attraction"; cf. Felsenstein, 1978). The third explanation postulates that two lines, both of which contained monosulcates, existed: one was paraphyletic to extant eudicots, and the monosulcate members of this line are now extinct; the other line included at the least all extant monosulcates. This third scenario implies the existence of yet unidentified lineages of monosulcates in the fossil record.

It has long been recognized by phylogenists that Magnoliidae sensu Cronquist are paraphyletic to monocots and eudicots. A cladistic study of basal angiosperms using morphological characters has corroborated this viewpoint (Donoghue & Doyle, 1989). Our study of *rbc*L sequences further demonstrates the paraphyly of the Magnoliidae. Takhtajan (1987) and Dahlgren (1989) removed the Ranunculales from the Magnoliidae and placed them in a higher category equal to the rest of the subclass. These plants lack several features used to define the Magnoliidae, e.g., spherical ethereal oil cells in the parenchymatous tissues and monosulcate pollen. In our analyses, the Ranunculales consistently fall into the strongly supported eudicot clade apart from the rest of the Magnoliidae sensu Cronquist.

The Nymphaeales are another member of the Magnoliidae that are often treated as an independent group of equal rank to the rest of the subclass (Thorne, 1992) or to all other monosulcate members of the subclass (i.e., excluding Ranunculales; Walker & Walker, 1984; Takhtajan, 1987). This study does not support such treatment. The Nymphaeales are only one of the major lineages in monosulcate Magnoliidae, and furthermore, several other taxa, Amborellaceae, Austrobaileyaceae, and Illiciales, share a close, unique phylogenetic relationship with them.

The enigmatic genus *Ceratophyllum* forms its own clade and is sister to all other angiosperms when outgroups to the angiosperms are included, but when only angiosperms are analyzed its highly divergent sequence is involved in two islands of equally parsimonious trees in which it occurs in radically different positions (Figs. 3, 4). The affinities of *Ceratophyllum* have been controversial, and most recent authors favored a relationship with *Cabomba* of the Cabombaceae (Cronquist, 1981; Takhtajan, 1980; Dahlgren, 1989). After a critical review of all the evidence, Les (1988) questioned this connection. The phylogenetic position of *Ceratophyllum* shown in this study largely corroborates Les's (1988; Les et al., 1991) proposition that the genus represents a vestige of the ancient angiosperms that diverged early from the line leading to most other modern taxa. From Aptian sediments in Victoria, Australia, and Albian and Cenomanian sediments in Kansas, North America, Dilcher (1989) reported fossil fruits similar to those of extant *Ceratophyllum* species; fossil leaves resembling those of modern *Ceratophyllum* were also found associated with the fruits. Possession of a suite of distinctive characters (partially sealed carpels, unitegmic ovules, branching pollen tubes, and lack of exine, vessels, and perianth) makes the genus anomalous among angiosperms.

No evidence, however, can be considered to give strong support for any of the placements of *Ceratophyllum* in our *rbc*L trees. The inclusion of distantly related outgroups (in particular, the highly divergent Gnetales) may be responsible for the placement of *Ceratophyllum* as sister to the rest of the angiosperms by introducing spurious synapomorphies. Nevertheless, in the search with nonflowering seed plants removed (Search C), *Cera-*

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FIGURE 5. One of the 186 maximum-parsimony (Fitch) trees found in a constraint experiment in which the Nymphaeales were specified as the sister of all other angiosperms. These trees are only 11 steps less parsimonious than the most parsimonious, unconstrained trees found with the same data matrix. The branch lengths are Fitch optimizations (ACCTRAN).

*tophyllum* remains as an outlier to the monosulcates and eudicots in the trees of one island (Fig. 3). In the trees from the other island, the genus is allied with *Canella* in the Magnoliales (Fig. 4), which seems unsatisfactory, both from the perspective of the long branches of *Ceratophyllum* and *Canella* and lack of corroboration from other evidence. In the topology constraint experiment (Search D), *Ceratophyllum* again ends up in another position that is potentially spurious (Fig. 5). Our overall conclusion is that the *rbc*L analyses do not definitively resolve the phylogenetic relationships of *Ceratophyllum*, but they do suggest, in agreement with Les's hypothesis (1988, 1991), that it is distantly related to all other extant angiosperms and may represent an ancient and highly modified taxon allied to the oldest angiosperms, which is consistent with its long fossil history.

### 2. PHYLOGENETICS OF THE MAGNOLIALES, LAURALES, PIPERALES, NYMPHAEALES, AND RANUNCULALES

The isolated position of Winteraceae has been recognized for some time (Bailey & Nast, 1943; Ehrendorfer et al., 1968; Thorne, 1968; Walker, 1976a; Takhtajan, 1980), and the family is placed independently in several classification systems (Walker & Walker, 1984; Takhtajan, 1987; Dahlgren, 1989; Thorne, 1992). A morphological cladistic study showed that Winteraceae fall outside of the "core" Magnoliales (Donoghue & Doyle, 1989). The family has several features that are not compatible with other members of Magnoliales, e.g., vesselless wood, poorly organized leaf venation, and ulcerate pollen shed in permanent tetrads. The Canellaceae are another family not securely placed in the Magnoliales (Donoghue & Doyle, 1989). A relationship between these two families emerges from this study as well as previous work. Leroy (1977) suggested that Winteraceae are allied to Canellaceae via the anomalous Madagascan genus *Takhtajania*; both have a compound unilocular ovary, a type of gynoecium rare in the Magnoliales. The two families (plus the Illiciales) were found to be associated in some of the equally most parsimonious trees in Donoghue & Doyle's (1989) study. Gottlieb et al. (1989) found that among members of Magnolianae and Piperales sensu Dahlgren, Winteraceae and Canellaceae share sesquiterpenoids of the drimane and rearranged drimane type, and at least two representatives of the drimane type occur only in these two families. A recent study of 26S rDNA also showed that these two families are related (Suh et al., 1992).

The other families of the Magnoliales, Annonaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, and Myristicaceae, are often recognized as "core" Magnoliales (Thorne, 1976; Walker, 1976a). Donoghue & Doyle's (1989) morphological cladistic study also identified this group. Our study of *rbc*L sequences offers moderate support for this group (Fig. 3). The Myristicaceae, traditionally regarded as an advanced member of Magnoliales (Walker, 1976b; Walker & Walker, 1984), occupy a weakly supported basal position in this clade (Fig. 3).

The anomalous magnoliaceous genus *Liriodendron* stands in an isolated position from the rest of the family, and its inclusion in the Magnoliaceae has been questioned by Barkley (1975). The relationship of *Liriodendron* to other magnoliaceous members is well supported in this study (Fig. 3). A reliable morphological character supporting monophyly of Magnoliaceae is their gynoecium, spirally arranged follicles on an elongate receptacle, which elsewhere is only found in Ranunculaceae. The mid-Cretaceous (Cenomanian) angiospermous fructification *Archaeanthus* provides evidence for a long history of this type of fruit (Dilcher & Crane, 1984). Another character defining the Magnoliaceae is their large stipules that enfold terminal buds. The rest of the Magnoliaceae are so homogenous that their taxonomy is notoriously difficult (Dandy, 1964; Law, 1984; Nooteboom, 1985), and *rbc*L sequences show little divergence among the genera (Qiu, Chase & Parks, unpublished).

In Laurales, *Hernandia* and *Gyrocarpus* have been placed in two unrelated families, Hernandiaceae and Gyrocarpaceae, by some (Walker & Walker, 1984; Takhtajan, 1987). Our study shows that the relationship between these two genera is strong even though their *rbc*L sequences are divergent (Fig. 3). Dahlgren's (1983, 1989) inclusion of these two genera in the Lauraceae is not supported by this study.

The Calycanthaceae and Idiospermaceae form a strongly supported clade, though resolution of their relationships to other lauralean families is poor. Interfamilial relationships within the Laurales are not well resolved (Fig. 3). Lack of several important taxa, such as *Trimenia*, *Gomortega*, *Atherosperma*, and other monimiaceous genera, may be a problem. Inclusion of these taxa in future studies should help to improve the resolution.

The relationship between Aristolochiaceae and Piperaceae/Saururaceae has not been consistently recognized. Takhtajan (1987) and Cronquist (1988) placed the two groups together, whereas Dahlgren (1989) and Thorne (1992) allied the Aristolochi-

aceae with the "core" Magnoliales rather than with the Piperales. Results from our study clearly favor association of the two groups.

The affinity of Lactoridaceae is an extensively debated issue. In the past, this family has been placed in the Magnoliales (Cronquist, 1981), Laurales (Takhtajan, 1980), Piperales (Walker & Walker, 1984; Thorne, 1992), or in its own order Lactoridales between the Magnoliales and Winterales (Dahlgren, 1989). A study of the family with numerical approaches suggested a magnolialean affinity (Lammers et al., 1986), but the proposition has been criticized by Carlquist (1990) on the basis of wood anatomy. Recent cladistic investigations using morphological data indicated a relationship to the Piperales (Dahlgren & Bremer, 1985; Donoghue & Doyle, 1989). A detailed comparative study of wood anatomy revealed that the Chloranthaceae, Piperaceae, and Lactoridaceae are similar in wood anatomy (Carlquist, 1990). In our analyses, support for a relationship of *Lactoris* to *Aristolochia* is weak, but alliance of the genus within Piperales is moderately supported (Fig. 3). *Aristolochia* has a rather divergent sequence, and more sampling in future studies may help to characterize better the affinities of the genus and *Lactoris*.

The Nymphaeales are distinct among primitive angiosperms in that they occupy a peculiar ecological niche and exhibit many characteristics of aquatic adaptation. How they are related to the rest of the Magnoliidae has been a long-standing issue in the phylogenetics of primitive angiosperms. In this study, we found the Nymphaeales are allied with several isolated taxa, Amborellaceae, Austrobaileyaceae, and Illiciales, whose relationships have also been widely debated. This topology is rather novel, but it is not drastically different from some previous ideas. Takhtajan (1980) and Cronquist (1981) suggested the Nymphaeales are derivatives of a woody ancestor with magnolialean features. The Austrobaileyaceae and Illiciales share many floral features with the Magnoliales and have been treated as members of that order in the past. The Amborellaceae are generally regarded as a basal member of the Laurales and have been placed near the Magnoliales (Cronquist, 1981). Hence, it is not unreasonable that these taxa form a group paraphyletic to Nymphaeales.

The Amborellaceae are a poorly studied monotypic family endemic to New Caledonia and have always been treated as a member of the Laurales. Bailey & Swamy (1948), however, found that the only species of the family, *Amborella trichopoda* Baill., lacks vessels and then questioned its placement in the Monimiaceae. Whether the angiosperms are primitively vesselless is an unresolved issue (Young, 1981; Donoghue & Doyle, 1989; Carlquist, 1992). It is possible that the Nymphaeales are secondarily vesselless (Cronquist, 1981). If vessellessness in primitive angiosperms is indeed due to secondary loss, this character may be of significant phylogenetic value in associating *Amborella* with the Nymphaeales. Another line of evidence supporting the relationship between *Amborella* and Nymphaeales is their lack of ethereal oil cells in parenchymatous tissues (Money et al., 1950; Cronquist, 1981). The ethereal oil cells are a characteristic feature of monosulcate Magnoliidae, and are otherwise found in all members. Finally, both Amborellaceae and Nymphaeales have granular pollen that has no or reduced endexine in the nonaperture regions of the exine, features that elsewhere are found only in the "core" Magnoliales, Trimeniaceae and some Chloranthaceae (Walker, 1976b). Although these "negative" characters need to be investigated further, they support a relationship between Nymphaeales and Amborellaceae.

The Illiciales stand as the only exception of a tricolpate pollen-bearing taxon among the monosulcate angiosperms. Previously, Walker & Doyle (1975) have highlighted their problematic aperture type. Huynh (1976, cited in Doyle & Hotton, 1991) revealed that the tricolpate condition in Illiciales is of a different type from that of eudicots; the three colpi are oriented according to Garside's rule, not Fischer's rule as in the latter. This implies that the tricolpate condition evolved independently in these two lineages. Our results support such interpretation. Leaf architecture (Hickey & Wolfe, 1975) and morphological cladistics (Donoghue & Doyle, 1989) also favor this hypothesis, though neither of these studies associates Illiciales with the particular group of monosulcate magnoliids as identified in this study. A relationship between Illiciales and Winteraceae has been proposed by some workers (Walker, 1976a; Donoghue & Doyle, 1989; Doyle et al., 1990) who relied partly on palynological evidence, yet such a relationship was not observed in investigations of chromosome number, leaf epidermis, and secondary compounds (Ehrendorfer, 1968; Baranova, 1972; Gottlieb et al., 1989). The one pollen character, coarsely reticulate and semitectate exine, that unites the two groups in Donoghue & Doyle's (1989) cladistic study has not been observed in *Walkeripollis*, the Early Cretaceous fossil pollen of putative winteraceous affinity (Doyle & Hotton, 1991).

The Austrobaileyaceae are yet another poorly studied family. They have been allied to Monimi-

aceae in Laurales (Bailey & Swamy, 1949) or Annonaceae of Magnoliales (Endress, 1980, 1983; Endress & Honegger, 1980). As noted by Cronquist (1981), the family has a combination of characters that make its placement in either order difficult: unilacunar nodes, opposite leaves, climbing habit, laminar stamens, hypogynous flowers, monosulcate pollen, and pluriovulate carpels. The relationship between Austrobaileyaceae and Illiciales identified in this study is supported by their similar sieve-element plastids (Behnke, 1988).

Given the extensive fossil record of Chloranthaceae (Couper, 1958; Kuprianova, 1967; Hughes et al., 1979; Muller, 1981; Upchurch, 1984; Walker & Walker, 1984; Friis et al., 1986; Chlonova & Surova, 1988), it may be safe to suggest that the family was more diverse in the past. A recent report of chloranthaceous fruits with anatropous ovules, instead of orthotropous ovules as in extant species, from Cenomanian sediments in eastern North America corroborates such a hypothesis (Pedersen et al., 1991). The modern family stands in a rather isolated position and has been placed in the Laurales (Thorne, 1992), Piperales (Cronquist, 1988), in its own order Chloranthales between Lactoridales and Piperales (Takhtajan, 1987), or between Winterales and Illiciales (Dahlgren, 1989). In this study, we found the Chloranthaceae are allied with Austrobaileyaceae, Illiciales, Amborellaceae, and Nymphaeales, but this position is weakly supported (Fig. 3). It has been suggested the Amborellaceae are related to the Chloranthaceae on the basis of floral morphology and anatomy (Endress, 1986a, 1987). Behnke (1988) also found Chloranthaceae share similar sieve-element plastids with Austrobaileyaceae and Illiciales.

Assignment of Ranunculales and other ranalian taxa such as Eupteleaceae, Nelumbonaceae, and Trochodendrales (Trochodendraceae and Tetracentracaeae) into two subclasses, the Magnoliidae (or Ranunculidae) and Hamamelidae by Takhtajan (1987) and Cronquist (1988) may have led to a belief that these taxa are distantly related. In our analyses, they form, together with several other taxa (Buxaceae, Gunneraceae, Platanaceae, Proteaceae, and Sabiaceae), a paraphyletic group at the base of the eudicots. In comparing vegetative and reproductive morphology, Nast & Bailey (1946) dissociated *Euptelea* from *Trochodendron* and *Tetracentron*, to which they have been frequently allied (Endress, 1986b). Examinations of pollen morphology and leaf architecture corroborated the isolated position of *Euptelea* (Praglowski, 1974; Wolfe, 1989). Nast & Bailey (1946) pointed out that the genus is of general ranalian affinity because it possesses several features of "the syndrome of primitive characters," such as apocarpous gynoecium, incompletely sealed carpels, and numerous stamens originating in centripetal sequence. They suggested that *Euptelea* is obviously not related to the ranalian families with monosulcate pollen and ethereal oil cells, but rather to those with tricolpate pollen and no ethereal oil cells (i.e., Ranunculaceae, Berberidaceae, Lardizabalaceae, Menispermaceae, and Trochodendraceae).

The Sabiaceae were tentatively placed in the Ranunculales by Cronquist (1981). This study shows that the family is not a member of the order, but occupies a basal position in the eudicots.

The exact relationships of Nelumbonaceae have not been certain, although their affinity to the Magnoliidae is generally recognized. Tricolpate pollen, roots with vessels, and production of benzyl-isoquinoline and aporphine alkaloids are among the characters that warrant removal of this family from Nymphaeales. Serological and cytological evidence shows the family does not belong to the Nymphaeales (Simon, 1971; Raven, 1975). These characters plus absence of ethereal oil cells suggest a relationship to basal eudicots rather than the monosulcate magnoliids. Both Donoghue & Doyle's (1989) morphological cladistic study and phytochemical evidence (Gottlieb et al., 1989) support such a position.

## 3. THE BASALMOST LINEAGE OF ANGIOSPERMS

Although the Ranalian Hypothesis that Magnoliidae represent the primitive angiosperms has been generally accepted, which lineage in the subclass is the most primitive remains an extensively debated issue (Friis et al., 1987). Woody Magnoliales with large strobiloid flowers and herbaceous Piperales with diminutive and simple flowers both have their proponents. Reports of chloranthoid and other non-magnolialean reproductive and vegetative structures in the Early and Middle Cretaceous (Couper, 1958; Dilcher, 1979; Krassilov et al., 1983; Upchurch, 1984; Walker & Walker, 1984; Friis et al., 1986; Crane et al., 1986; Crane, 1989; Taylor & Hickey, 1990; Pedersen et al., 1991) challenge the status of Magnoliales as the most primitive angiosperms. Cladistic studies finding that Gnetales and Bennettitales are equally closely related to angiosperms (Crane, 1985; Doyle & Donoghue, 1986) add further controversy to the debate.

Paleobotany has played an instrumental role in

elucidating the early evolution of angiosperms. A large body of fossil evidence of early angiosperms has been gathered in the last several decades, documenting presence of several major lineages of primitive angiosperms in the Early and Middle Cretaceous: Magnoliales, Laurales, Piperales, Nymphaeales, Ranunculales, and "lower" Hamamelidae (Couper, 1958; Doyle, 1969; Muller, 1970, 1981, 1984; Doyle & Hickey, 1976; Doyle et al., 1977, 1990; Hickey & Doyle, 1977; Dilcher, 1979; Hughes et al., 1979; Krassilov et al., 1983; Walker et al., 1983; Dilcher & Crane, 1984; Upchurch, 1984; Walker & Walker, 1984; Crane et al., 1986; Friis et al., 1986; Ward et al., 1989; Drinnan et al., 1990, 1991; Hughes & McDougall, 1990; Taylor & Hickey, 1990; Herendeen, 1991; Pedersen et al., 1991). These studies have greatly expanded our knowledge of early angiosperm evolution but have not answered the question of the origin of angiosperms. Further exploration of sediments of the preceding Early Cretaceous and Late Jurassic ages will be necessary before firm conclusions regarding the origin of the angiosperms are reached (Hughes & McDougall, 1987, 1990).

In a cladistic study of mostly morphological data, Donoghue & Doyle (1989) identified the Magnoliales as the basalmost lineage among angiosperms. However, they found that Nymphaeales are basal in trees only slightly less parsimonious (1 step longer or 0.56% less parsimonious; the length of their shortest trees was 178 steps). Our constraint experiment (Fig. 5) demonstrated a similar small loss of parsimony for this alternate hypothesis (0.32% less parsimonious; see Results). Hamby & Zimmer (1992) reported that Nymphaeales and Piperales are paraphyletic to other angiosperms in their investigation using ribosomal RNA sequences, but many important taxa were absent from their study. Martin & Dowd (1991) found Illiciales to be sister to all other angiosperms in their study of *rbc*S amino acid sequences. In our analyses, we found only weak support for relationships at the base of angiosperms (Fig. 3). Thus, the *rbc*L results, in spite of being resolved in favor of *Ceratophyllum* if outgroups were included, do not strongly support or refute any hypothesis of which group of Magnoliidae is sister to all other angiosperms.

## 4. RELATIONSHIPS OF THE MAGNOLIIDAE TO MONOCOTS AND EUDICOTS

The relationship between Magnoliidae and monocots has been discussed extensively (Dahlgren & Clifford, 1982; Dahlgren et al., 1985). It is widely believed that the two groups are closely related. Hegnauer (1977) reported that the Magnoliidae (including Ranunculales) and monocots exclusively use the tyrosine-pathway for synthesizing cyanogenic compounds, whereas other dicots exploit phenylalanine for the same purpose. In studying the distribution and biosynthesis of shikimate-derived compounds, Kubitzki & Gottlieb (1984) found that angiosperms are essentially composed of two groups, the "magnolialean block" (magnoliids, monocots, and caryophyllids) and the "rosiflorean block" (the rest of the dicots). Previously, different pairs of the magnoliids and monocots have been proposed to account for the origin of the monocots: Ranunculales/Piperales vs. Alismatales (Bessey, 1915), Nymphaeales vs. Alismatales (Takhtajan, 1969; Cronquist, 1968), Piperales vs. Arales (Burger, 1977), and Annonales vs. Dioscoreales (Dahlgren et al., 1985). Considering the heterogeneity of the Magnoliidae and a great number of similarities between the subclass and monocots (Dahlgren & Clifford, 1982; Dahlgren & Bremer, 1985), it is not surprising to see such diverse opinions about their relationship. Most, if not all, of these similarities are based on character states that are potentially symplesiomorphic or due to parallel evolution.

Although resolution of relationships at the base of angiosperms is weak in our study, several groups may be removed from the list of possible close allies to the monocots. The Ranunculales are a member of a well-supported eudicot clade and do not show any relationship to the monocots. The Nymphaeales alone are unlikely to be sister to the monocots because they show a strongly supported relationship to Amborellaceae, Austrobaileyaceae, and Illiciales. Any other major lineage of the Magnoliidae could be placed as a sister group to the monocots with only an insignificant loss of parsimony.

Monophyly and origin(s) of the eudicots have been subject to a remarkable diversity of opinions. Interpretation of traditional phylogenetic diagrams such as those of Takhtajan (1959, 1969, 1980, 1987) would lead to a conclusion that eudicots are polyphyletic and composed of several lineages independently derived from various monosulcate angiosperms with magnoliid features. Under the assumption that eudicots are derived from the monosulcates, Walker & Walker (1984) suggested that the monosulcate magnoliid families Winteraceae, Illiciaceae, Schisandraceae, and Aristolochiaceae have ties with the subclasses Ranunculidae and Caryophyllidae and that the Lactoridaceae,

Piperaceae, Saururaceae, and especially Chloranthaceae are linked to the Hamamelidae and through it to remaining dicots. In a cladistic investigation of basal angiosperms using morphological characters, Donoghue & Doyle (1989) concluded that Ranunculidae, Nelumbonaceae, and paleoherbs (including Lactoridaceae, Aristolochiaceae, Piperaceae, Saururaceae, Nymphaeaceae, Cabombaceae, and monocots) are more closely related to the Hamamelidae and other "higher" dicots than the Magnoliales and Chloranthaceae. Furthermore, they found that in some of their most parsimonious trees ranunculids and hamamelids form a monophyletic group sister to the paleoherbs, whereas in others the ranunculids are dissociated from the hamamelids and united with the paleoherbs. Doyle & Hotton (1991) reported that the oldest tricolpate pollen from the late Barremian–early Aptian of Gabon exhibits two features of typical paleoherb pollen: the sculpture consists of intermixed large and small lumina (heterobrochate) and varies from coarser at the equator to finer at the poles (graded).

The monophyly of eudicots (dicots with tricolpate and derived pollen types, including Nelumbonaceae and Takhtajan's Ranunculidae but excluding Illiciales) is strongly supported by this study. Fossil evidence from the Potomac group in eastern North America shows that all tricolpate pollen and derived types can be traced back to a morphologically generalized complex of tectate-reticulate tricolpate pollen, thus corroborating the hypothesis of single origin of the eudicots (Wolfe et al., 1975). This type of tectate-reticulate tricolpate pollen is found in the extant Rananculales, Platanaceae, and Trochodendrales (Muller, 1984), which is consistent with placement of these taxa at the base of eudicots in the *rbc*L trees (Figs. 1–4; also see Chase et al., 1993).

Many basal eudicots are wind-pollinated, for example, Buxaceae, Eupteleaceae, Menispermaceae, Platanaceae, Tetracentraceae, and possibly Gunneraceae and Trochodendraceae (Crane et al., 1991). Environmental factors such as the increasing aridity in a period immediately after the Barremian (Doyle et al., 1977; Hickey & Doyle, 1977), when tricolpate pollen first appeared (Hughes & McDougall, 1990; Doyle & Hotton, 1991), might have played a critical role in the rise of eudicots (Walker & Walker, 1984). The preponderance of wind-pollination in basal eudicots suggests that the group could be primitively wind-pollinated. Further investigation of other wind-pollinated members of the Ranunculales and "lower" Hamamelidae is needed before we have adequate information to address this question.

## Conclusions

This study of nucleotide sequences of the plastid protein-coding gene *rbc*L has identified the same major lineages as have many classification systems and previous cladistic studies of the Magnoliidae: (i) Magnoliales, (ii) Laurales, (iii) Piperales, (iv) Nymphaeales, and (v) Ranunculales. The exact familial composition of some of these clades is significantly different from any previous hypothesis. The most conspicuous difference is that Amborellaceae, Austrobaileyaceae, and Illiciales are strongly supported as members of the Nymphaeales clade. The relationship of these anomalous woody taxa to the Nymphaeales has only weak corroboration of shared absent features. Another novel feature of our results is that angiosperms fall into two monophyletic groups corresponding to the general pollen types of monosulcate and tricolpate, and they show a sister-group relationship. Our finding of the monophyletic eudicots lends strong support to pollen characters as major synapomorphies for these angiosperms. In contrast, we cannot identify any nonmolecular character to define the weakly supported monosulcate clade. Resolution of relationships at the base of angiosperms is low. The position of Ceratophyllaceae as a sister group to all other angiosperms is likewise controversial, but it is supported, though not unequivocally, by the fossil evidence and the distinctive morphology of these aquatic plants.

We conclude that our molecular survey of putatively basal angiosperms gains great support from the congruence of the groups identified in this study with those recognized in classification systems and recent cladistic analyses of nonmolecular data. Our analyses of the *rbc*L sequence data were conducted merely under the criterion of parsimony, and did not rely on any previous hypothesis of evolution of morphological characters or relationships among basal angiosperms. We take this to be an indication that the molecular character systems contain historically relevant information. The general relationships among basal angiosperms, as well as composition of certain clades (e.g., Nymphaeales) identified in our *rbc*L trees, are novel and intriguing, and we suggest that they be considered as alternatives to the traditional ideas about the phylogeny of the early angiosperms. Ironically, this molecular investigation adds more controversy instead of providing solutions to the questions surrounding early angiosperm evolution. A complete understanding of the origin of angiosperms certainly requires multidisciplinary studies of both fossil and extant plants with morphological and molecular approaches.

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# PHYLOGENETIC HYPOTHESES FOR THE MONOCOTYLEDONS CONSTRUCTED FROM *rbc*L SEQUENCE DATA[1]

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## Abstract

DNA sequences for the plastid locus that encodes the large subunit of ribulose 1,5-bisphosphate carboxylase oxygenase (*rbc*L) were determined for 18 species of monocotyledons in 15 families. These data were analyzed together with sequences for 60 other monocot species in a total of 52 families by the maximum likelihood method producing one, presumably optimal, topology. An additional 26 species were added (104 total monocot species) and analyzed by the parsimony method with an outgroup of 18 dicot species producing 109 trees of 3,932 steps. The *rbc*L data show at least moderate support for seven lineages corresponding to the following orders, superorders, or combinations: Arecanae; Asparagales (excluding Hypoxidaceae) plus Iridaceae; Cyclanthanae plus Pandananae; Dioscoreales; Orchidales; Typhales; and Zingiberanae. Six clades corresponding to families or genera are well supported, including: Agavaceae, Asphodelaceae, Bromeliaceae, Hypoxidaceae, Poaceae, and *Tradescantia*. The two, earliest diverging multispecies clades in our *rbc*L phylogenies, Alismatanae and Aranae, are only weakly supported, and Bromelianae, Commelinanae, and Lilianae are paraphyletic. In all analyses *Acorus calamus* is phylogenetically isolated as the sister species to the remaining species of monocotyledons.

Innovations for the manipulation of nucleic acids and advances in computer technology now permit phylogenetic analysis of homologous sequences of DNA from large numbers of organisms. These base-to-base comparisons of nucleotides afford the highest possible resolution of inherited mutations in DNA molecules and can be applied to questions of higher-order plant systematics. A locus that has been selected for such studies by molecular systematists is the plastid gene that encodes the large subunit of ribulose 1,5-bisphosphate carboxylase/oxygenase (*rbc*L). Phylogenetic reconstructions for lineages of monocotyledons based on *rbc*L sequence data have been attempted previously for: (1) Arecaceae (Wilson et al., 1990); (2) Bromeliaceae (Clark et al., in prep.); (3) Poaceae (Doebley et al., 1990); and (4) Zingiberales (Smith et al., 1993). These initial attempts met with a disappointing lack of resolution, in some cases because of the low substitution rate of *rbc*L, but strongly suggested that these data would have greater phylogenetic utility when applied to more divergent lineages. Our goal here was to reconstruct higher-order phylogenetic relationships among the mono-

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cotyledons using DNA sequence data from the *rbc*L locus for a set of species that represented the breadth of taxonomic diversity in the group.

## Materials and Methods

DNA sequences of *rbc*L from 104 species in 52 of 104 monocot families were analyzed (see Appendix in this issue for species, locations of vouchers, sequencing methods, extent of sequences, and authors). Eighteen of those sequences (Table 1) were produced specifically for this study by the following methods. Total DNA was extracted from fresh leaf tissue by the method of Doyle & Doyle (1987) for 16 species, the method of Palmer (1986) for *Cyperus alternifolius*, and the method of Jarrell et al. (1992) for *Lemna minuscula*. Approximately 1 μg of each DNA preparation was used to provide template for *Taq*-mediated amplification of the *rbc*L gene using the protocol provided with *Taq* DNA polymerase by the supplier (Promega Corp.). The primers for the reaction were two highly conserved sequences from the *rbc*L coding region of *Spinacia oleracea*. The 5′ primer consisted of the first 30 base pairs of that sequence and the 3′ (reverse) primer corresponded to positions 1351 to 1380 on the complementary strand. Amplifications utilizing these primers produced 1,320 base pairs of the coding sequence of *rbc*L. Primers that are external to the coding sequence occasionally resulted in successful amplifications of more of the *rbc*L coding sequence. For *Sparganium americanum*, a 27 base pair sequence at the promoter region for *rbc*L derived from positions 53742–53768 in the plastid genome of *Oryza sativa* was used as the 5′ primer. For *Gymnostachys anceps*, *Tradescantia* aff. *pallida*, and *Typha latifolia*, a 24 base pair sequence at a ribosome control site downstream of the coding sequence derived from positions 59146–59123 (complement) in the plastid genome of *Nicotiana tabacum* was used as the 3′ primer. Up to 1,428 base pairs of *rbc*L were produced, depending on the primers that were used in the amplification reactions. For the *rbc*L sequences from the monocotyledons analyzed here, 5.7% of the sequence data was missing largely because of the use of internal primers in the amplification reactions.

Single-stranded DNA was produced in a second round of amplification using the double-stranded product as template and the two primers individually. These single-stranded products were precipitated (7.5% polyethylene glycol-8000, 0.94 M NaCl), the DNA pellets were washed twice with ethanol, and sequencing was accomplished by the dideoxynucleotide chain-termination method using a set of conserved, synthetic, internal *rbc*L primers (obtained from G. Zurawski, DNAX Corp.). Both the *rbc*L coding strand and the complementary strand were sequenced for all species. The 18 *rbc*L sequences produced for this study were entered into "GenBank" under the accession numbers listed in Table 1.

The maximum likelihood method of phylogenetic analysis was selected for use here because it is less biased by the heterogeneous nucleotide substitution rates that have been observed for *rbc*L among different lineages of monocotyledons (Gaut et al., 1992) than are other methods (Felsenstein, 1981). Furthermore, under this method, likelihood scores may be calculated for alternate topologies and subjected to comparative tests of statistical significance. However, only a subset of the entire *rbc*L database could be analyzed since the method is computer-intensive. [To establish an estimate of the computer burden, a maximum likelihood analysis of 79 *rbc*L sequences using the program, DNAML in PHYLIP 3.42 (Felsenstein, 1991), was executed on a CRAY "Y-MP8/864" supercomputer. The analysis spanned 11 days with a run time of about 51 CPU hr. At this speed, ten executions of the program with different input orders (typically recommended) of the 79 *rbc*L sequences would have required over three months of real time utilizing more than 20 CPU *days* on this machine.] Consequently, 78 of the original 104 monocot species were selected for maximum likelihood analysis with *Saururus cernuus* as the outgroup (79 species total). Each of the following taxa, Agavaceae, Arecaceae, Bromeliaceae, Nolinaceae, Poaceae, and Zingiberales, invariably constituted a monophyletic lineage in preliminary phylogenetic analyses that included multiple species in each. The subset was thus selected to contain representatives from each of the 52 families while excluding some of the multiple species in these six taxa, preserving the potential for investigating higher order relationships. The species that were retained in the subset are: Agavaceae—*Manfreda maculosa* and *Yucca recurvifolia*; Arecaceae—*Caryota mitis*, *Phoenix reclinata*, and *Serenoa repens*; Bromeliaceae—*Aechmea chantinii* and *Tillandsia elizabethae*; Nolinaceae—*Nolina* (*Beaucarnea*) *recurvata*; Poaceae—*Oryza sativa* and *Zea mays*; and Zingiberales—*Calathea loeseneri*, *Costus barbatus*, *Globba curtisii*, *Hedychium gardnerianum*, *Heliconia latispatha*, *Maranta leuconeura*, *Musa cavendishii*, *Orchidantha fimbriata*, *Phenakospermum guyannense*, *Ravenala madagascariensis*, and *Tapeinocheilos ananassae*.

TABLE 1. Eighteen species for which *rbc*L was sequenced for this study. Vouchers (herbaria), accession numbers for the *rbc*L sequences submitted to GenBank, superordinal, ordinal, and familial alignments are given. Identities for the remaining 104 species that were analyzed may be found in the Appendix for this issue.

| Species | Vouchers (herbaria) | Family | GenBank accession |
|---|---|---|---|
| Aranae | | | |
| Arales | | | |
| *Acorus calamus* L. | *French 232* (CH) | Acoraceae | M91625 |
| *Gymnostachys anceps* R. Br. | *Howard 4325* (FTG) | Araceae | M91629 |
| *Pistia stratiotes* L. | *French 233* (CH) | Araceae | M96963 |
| *Lemna minuscula* Herter | *Duvall 19920501* (UCR) | Lemnaceae | M91630 |
| Bromelianae | | | |
| Typhales | | | |
| *Typha latifolia* L. | *Bradley 24974* (GMUF) | Typhaceae | M91634 |
| *Sparganium americanum* Nutt. | *Chase 257* (NCU) | Sparganiaceae | M91633 |
| Commelinanae | | | |
| Commelinales | | | |
| *Tradescantia* aff. *pallida* | *Bradley 24980* (GMUF) | Commelinaceae | L05041 |
| *Tradescantia zebrina* hort. ex Bosse | *Bradley 24980* (GMUF) | Commelinaceae | L05042 |
| Cyperales | | | |
| *Cyperus alternifolius* L. | *Duvall 19920602* (UCR) | Cyperaceae | M91627 |
| Lilianae | | | |
| Asparagales | | | |
| *Aloe vera* (L.) Burm. | *Bradley 24977* (GMUF) | Asphodelaceae | L05029 |
| *Haworthia subfasciata* Baker | *Bradley 24978* (GMUF) | Asphodelaceae | L05035 |
| *Chlorophytum comosum* (Thunb.) Jacques | *Bradley 7331* (GMUF) | Anthericaceae | L05031 |
| *Clivia miniata* Regel | *Bradley 24976* (GMUF) | Amaryllidaceae | L05032 |
| *Nolina* (*Beaucarnea*) *recurvata* (Lem.) Hemsl. | *Peterson 12606* (US) | Nolinaceae | L05030 |
| Liliales | | | |
| *Iris* ×*germanicum* L. | *Bradley 25976* (GMUF) | Iridaceae | L05037 |
| *Medeola virginiana* (L.) Merrill | *Bradley 24972* (GMUF) | Uvulariaceae | M91613 |
| Zingiberanae | | | |
| Zingiberales | | | |
| *Maranta leuconeura* E. Morris | *Bradley 24979* (GMUF) | Marantaceae | L05040 |
| *Hedychium gardnerianum* Ker Gawl. | *Bradley 24975* (GMUF) | Zingiberaceae | M91628 |

The analysis was executed on the fastest existing computer, the Touchstone Delta Parallel Processing Supercomputer, using "fastDNAml version 1.0.3" (Olsen et al., 1992). Thirty-three replications of the analysis were performed with different randomly determined orders of input. The "categories option," which permits specification of different substitution rates by codon position, was invoked using relative rates of 1.00, 0.85, and 5.80 for first, second, and third codon positions, respectively. These values are based on reported substitution rates at each codon position (Clegg et al., 1986; Ritland & Clegg, 1987). Regional and local branch swapping were employed. This portion of the analysis, which included data from 74 of the 79 species, consumed 125 hours of computer time.

After the initial analysis was performed, the remaining five species (*Aletris farinosa*, *Burmannia biflora*, *Sparganium americanum*, *Stegolepis allenii*, and *Typha latifolia*; total species: 79) with equivocal phylogenetic positions in preliminary analyses were added to the optimal topology from the previous step with 50 (of 120 possible) random

TABLE 2. Distribution of polymorphic sites, constant sites, and sites shared by two or more species (i.e., informative sites), among codon positions of *rbc*L. Sites are calculated for 1,428 base pairs and 79 species. Base substitutions were optimized on the topology of Figures 4 and 5.

| | Codon position | | | Total sites |
|---|---|---|---|---|
| | First | Second | Third | |
| Polymorphic sites | 221 | 210 | 430 | 861 |
| Constant sites | 255 | 266 | 46 | 567 |
| Informative sites | 137 | 124 | 394 | 655 |

input orders. Rearrangements of the optimal topology from this step were performed to arrive at a final result. Kishino & Hasegawa (1989) tests of the likelihood scores associated with topologies produced by each step of the analysis (available from M. Duvall on request) were performed.

Bootstrap and decay analyses were implemented with PAUP Version 3.0s (Swofford, 1991) on a Macintosh IIfx for the *rbc*L data set from 78 species of monocots. A set of 18 trees of length 3,117 was determined with more than ten replications of the input order. Trees one step longer (486 trees) and two steps longer (6,237 trees) were also determined. (An attempt to determine all trees up to four steps longer using a Macintosh Quadra 700 was aborted after 13.8 days of continuous execution. The analysis produced 14,873 trees occupying over 6 Megabytes of memory and was estimated to be 10% complete. Available computer memory was the limiting factor so that the time to perform read-write operations of treefiles from external memory became prohibitive.) Bootstrap analysis with 200 subsamples of the original data matrix was performed with local (i.e., "nearest neighbor interchange" or "NNI") branch swapping.

Three tests to ascertain the effect of constraining topologies so that selected species occupied monophyletic clades were conducted. The selected species groups were: (1) Commelinanae (13 spp.); (2) Alismatanae (4 spp.), and Aranae (4 spp.), together with *Acorus calamus*; and (3) each of nine superorders sensu Dahlgren et al. (1985). These constraints were imposed on parsimony analyses with 10 replications of the input order and NNI branch swapping.

For pragmatic reasons the parsimony method was selected for larger-scale analysis of *rbc*L sequences (104 monocot species). Eighteen dicot species were selected as an outgroup as suggested by a more inclusive analysis of angiosperms (Chase et al., 1993). Ten replications of the input order were executed with the "steepest descent" option invoked and global ("tree-bisection and reconnection" or "TBR") branch swapping employed. All equally most-parsimonious trees were saved.

## RESULTS

Of the 1,428 bases analyzed for 79 species, 861 were polymorphic and 50% of these were at third codon positions (Table 2). Of the 861 polymorphic sites, 655 were shared by two or more species and of these, 60% were at third codon positions.

The results of our phylogenetic analyses show greater congruence with the taxonomic system of Dahlgren et al. (1985) than with other contemporary systems (reviewed in Goldberg, 1989). References to taxa in this report thus follow that system.

The topology resulting from maximum likelihood analysis (Fig. 1) had an associated likelihood score of −18,878.21. Note that other topologies exist which have likelihood scores that are not significantly different from that of Figure 1. Bootstrap values and decay indices for analyses of 79 species are given (Fig. 2, Table 3). Recall that only trees up to two steps longer than the shortest trees were determined so that clades supported with decay indices of two may also be supported at higher,

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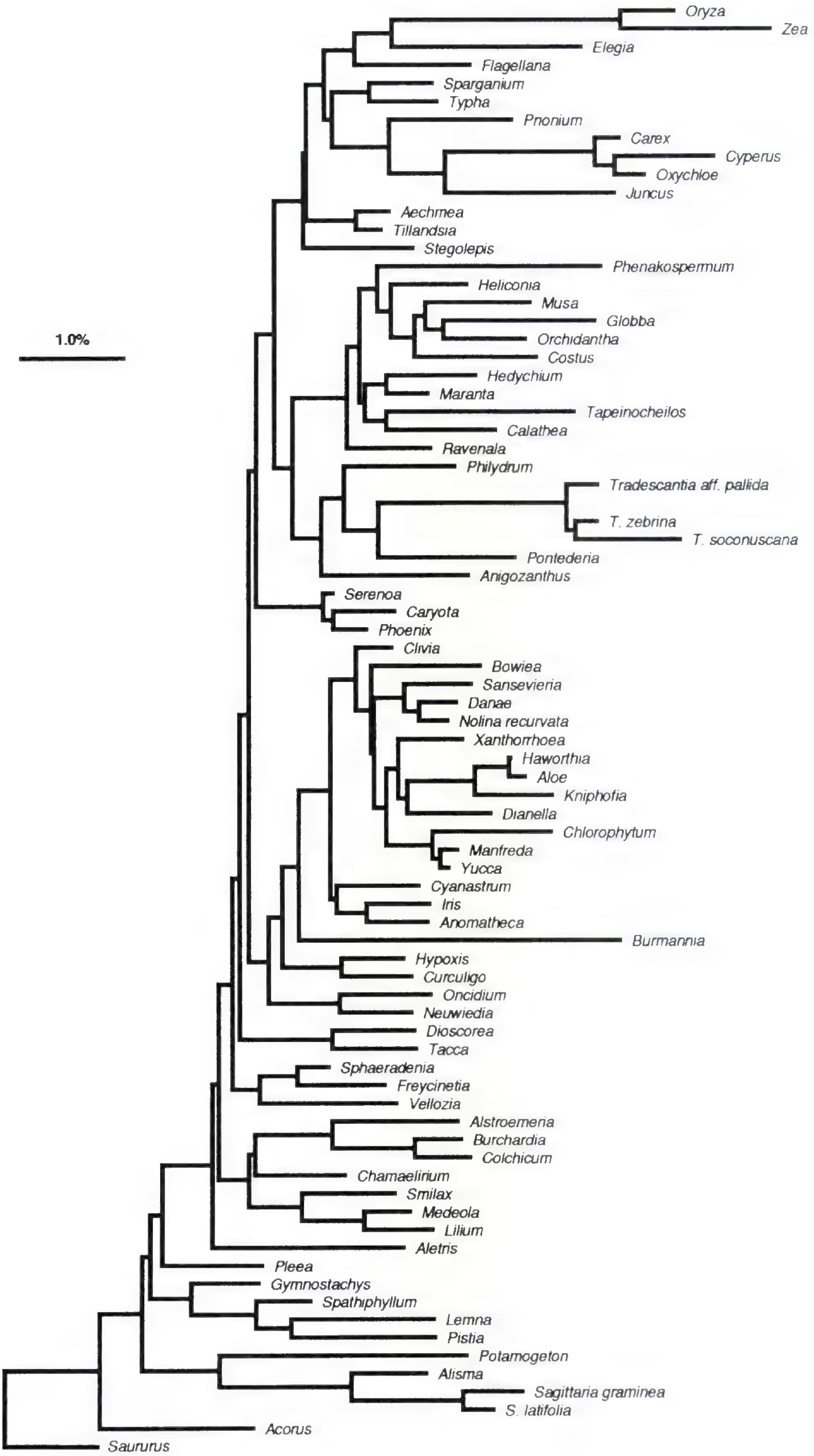
FIGURE 1. Topology for 78 monocotyledons and the outgroup dicotyledon *Saururus cernuus* (79 spp. total) produced by the maximum likelihood method with a log likelihood of −18,878.21. The analysis was executed using the computer program fastDNAml 1.0.3 (Olsen et al., 1992), on the Touchstone Delta Parallel Processing Supercomputer, the fastest existing computer. The initial phase of the analysis included 74 of these species, employed regional and local branch swapping, specified substitution rates of 1.00, 0.85, and 5.80 for first, second, and third codon position substitutions, respectively, under the "categories" option, was performed with 33 replications of the input order, and consumed more than 125 hours of supercomputer time. Five additional species, *Aletris farinosa*, *Burmannia biflora*, *Sparganium americanum*, *Stegolepis allenii*, and *Typha latifolia*, were added more than 50 times to the initial topology with the largest log likelihood score. Additional rearrangements of the tree with the largest likelihood score produced the tree shown here. Scale bar indicates 1.0% maximum likelihood distance units as calculated under the assumptions specified above. Species are indicated by genera only. For complete binomials see Appendix in this issue.


1.0%
Oryza
Zea
Elegia
Flagellana
Sparganium
Typha
Pronium
Carex
Cyperus
Oxychloe
Juncus
Aechmea
Tillandsia
Stegolepis
Phenakospermum
Heliconia
Musa
Globba
Orchidantha
Costus
Hedychium
Maranta
Tapeinocheilos
Calathea
Ravenala
Philydrum
Tradescantia aff. pallida
T. zebrina
T. soconuscana
Pontederia
Anigozanthus
Serenoa
Caryota
Phoenix
Clivia
Bowiea
Sansevieria
Danae
Nolina recurvata
Xanthorrhoea
Haworthia
Aloe
Kniphofia
Dianella
Chlorophytum
Manfreda
Yucca
Cyanastrum
Iris
Anomatheca
Burmannia
Hypoxis
Curculigo
Oncidium
Neuwiedia
Dioscorea
Tacca
Sphaeradenia
Freycinetia
Vellozia
Alstroemeria
Burchardia
Colchicum
Chamaelirium
Smilax
Medeola
Lilium
Aletris
Pleea
Gymnostachys
Spathiphyllum
Lemna
Pistia
Potamogeton
Alisma
Sagittaria graminea
S. latifolia
Acorus
Saururus

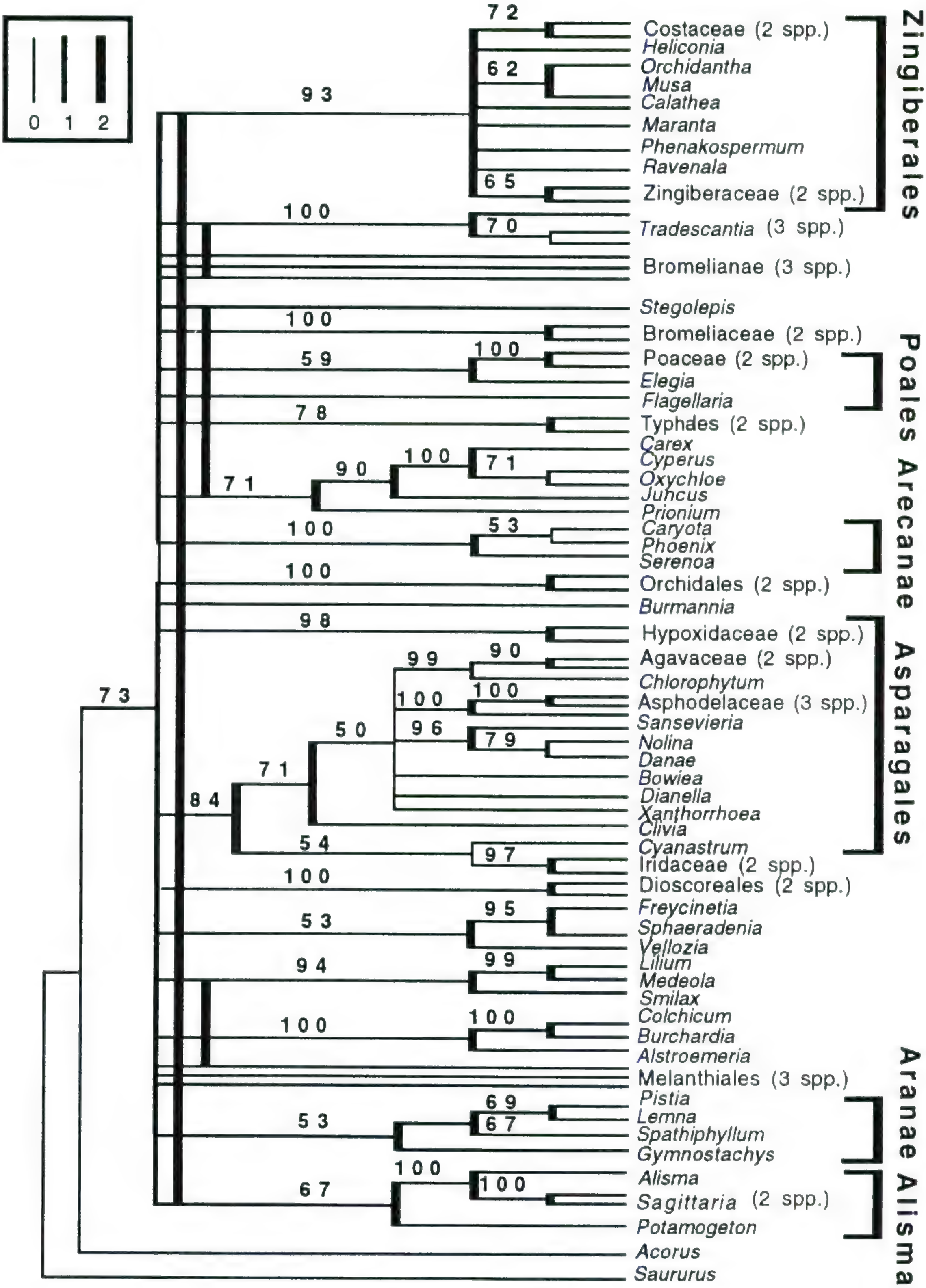

0 1 2
Zingiberales
Poales
Arecanae
Asparagales
Aranae
Alismatanae
Costaceae (2 spp.)
Heliconia
Orchidantha
Musa
Calathea
Maranta
Phenakospermum
Ravenala
Zingiberaceae (2 spp.)
Tradescantia (3 spp.)
Bromelianae (3 spp.)
Stegolepis
Bromeliaceae (2 spp.)
Poaceae (2 spp.)
Elegia
Flagellaria
Typhales (2 spp.)
Carex
Cyperus
Oxychloe
Juncus
Prionium
Caryota
Phoenix
Serenoa
Orchidales (2 spp.)
Burmannia
Hypoxidaceae (2 spp.)
Agavaceae (2 spp.)
Chlorophytum
Asphodelaceae (3 spp.)
Sansevieria
Nolina
Danae
Bowiea
Dianella
Xanthorrhoea
Clivia
Cyanastrum
Iridaceae (2 spp.)
Dioscoreales (2 spp.)
Freycinetia
Sphaeradenia
Vellozia
Lilium
Medeola
Smilax
Colchicum
Burchardia
Alstroemeria
Melanthiales (3 spp.)
Pistia
Lemna
Spathiphyllum
Gymnostachys
Alisma
Sagittaria (2 spp.)
Potamogeton
Acorus
Saururus

TABLE 3. Support for clades corresponding to taxa sensu Dahlgren et al. (1985) by *rbc*L data for 78 species of monocotyledons. Parenthetical numbers immediately following taxa indicate the number of species analyzed. Bootstrap values (200 replicates) and decay indices (up to two steps longer than the most parsimonious topologies) are given. Clades supported with decay indices of two may also be supported at a higher, undetermined, decay index. Also given are the numbers of substitution events supporting each lineage and the number of nonhomoplastic synapomorphies (appearing parenthetically following branch lengths) in the maximum likelihood topology (Fig. 1).

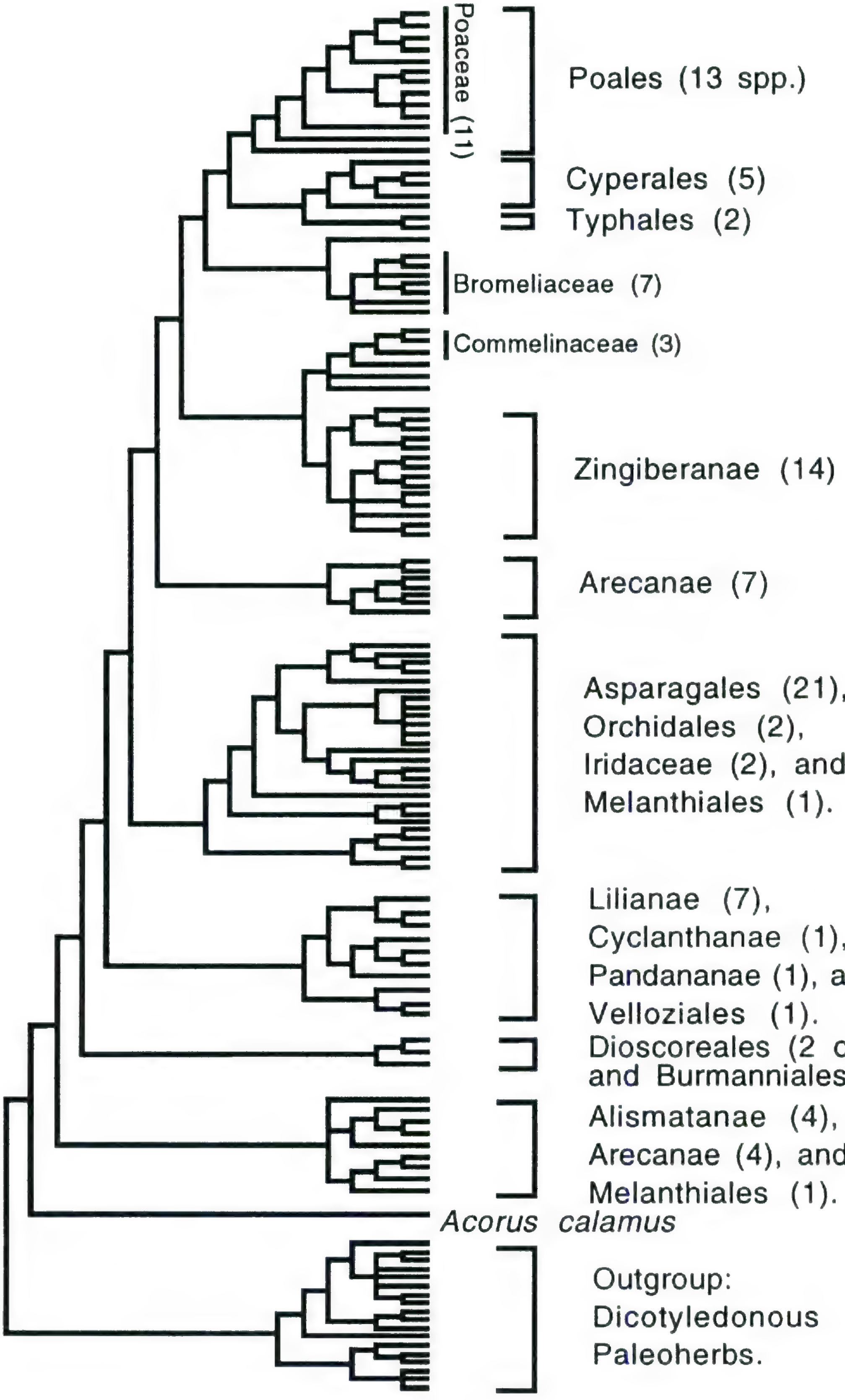
| Taxa (number of species) | Bootstrap values (%) | Decay indices | Lengths |
|---|---|---|---|
| Alismatanae (4) | 67 | ≥ 2 | 37 (3) |
| Aranae (4) | 53 | ≥ 2 | 14 (1) |
| Arecanae (3) | 100 | ≥ 2 | 31 (4) |
| Bromelianae (8) | < 50 | 0 | — |
| Bromeliaceae (2) | 100 | ≥ 2 | 14 (0) |
| Typhales (2) | 78 | ≥ 2 | 21 (11) |
| Commelinanae (13) | < 50 | 0 | — |
| Cyperales (5) | 71 | ≥ 2 | 26 (1) |
| Poales (3 of 4) | 59 | ≥ 2 | 21 (2) |
| Poaceae (2) | 100 | ≥ 2 | 66 (7) |
| *Tradescantia* (3) | 100 | ≥ 2 | 48 (3) |
| Cyclanthanae (1) plus Pandananae (1) | 95 | ≥ 2 | 13 (1) |
| Lilianae (32) | < 50 | 0 | — |
| Asparagales (14 of 16) plus Iridaceae (2) | 84 | ≥ 2 | 13 (1) |
| Agavaceae (2) | 90 | ≥ 2 | 3 (0) |
| Asphodelaceae (3) | 100 | ≥ 2 | 21 (1) |
| Hypoxidaceae (2) | 100 | ≥ 2 | 18 (1) |
| Dioscoreales (2 of 3) | 98 | ≥ 2 | 27 (2) |
| Orchidales (2) | 100 | ≥ 2 | 23 (1) |
| Zingiberanae (11) | 93 | ≥ 2 | 20 (1) |
| Costaceae (2) | 72 | ≥ 2 | — |
| Zingiberaceae (2) | 65 | ≥ 2 | — |
| Monocotyledons excluding *Acorus calamus* (77 spp.) | 73 | ≥ 2 | 13 (1) |

undetermined, values. Seven lineages found in the maximum likelihood tree that have associated bootstrap values at or above 78% and decay indices greater than or equal to two correspond to orders, superorders, or combinations of these. These are: (1) Arecanae (3 spp.); (2) Asparagales (excluding Hypoxidaceae: 14 spp.) plus Iridaceae (2 spp.); (3) Cyclanthanae plus Pandananae (1 spp. each); (4) Dioscoreales (2 of 3 spp.); (5) Orchidales (2 spp.); (6) Typhales (2 spp.); and (7) Zingiberanae (11 spp.). Six clades of confamilial or congeneric species are supported by the *rbc*L data at a bootstrap value of at least 90% and a decay index of at least two including: Agavaceae, Asphodelaceae, Bromeliaceae, Hypoxidaceae, Poaceae, and *Tradescantia*.

Parsimony analysis of 122 species produced a set of 109 equally parsimonious trees of 3,932 steps over the 1,428 characters (see overview of strict consensus tree, Fig. 3). These trees have consistency indices (excluding uninformative characters) of 0.267 (the low value reflecting the large number of species) and retention indices of 0.633. One of these 109 trees was arbitrarily selected and is given in detail (Figs. 4, 5) to enumerate genera and illustrate comparative branch lengths.

←

FIGURE 2. Majority rule (50%) consensus tree for 79 species. The bootstrap analysis was conducted using PAUP 3.0s with 200 bootstrap subsamples of the data matrix. Percentage values for those branches occurring in at least 50% of the bootstrap topologies are shown. Selected taxa are identified. Branch lengths are arbitrary. Decay values up to two steps longer are indicated as vertical bars of varying thickness overlaid on the bootstrap topology. The thickest lines indicate clades supported in trees at least two steps longer. The thinnest lines indicate clades supported only in maximum parsimony trees.


Poaceae (11)
Poales (13 spp.)
Cyperales (5)
Typhales (2)
Bromeliaceae (7)
Commelinaceae (3)
Zingiberanae (14)
Arecanae (7)
Asparagales (21),
Orchidales (2),
Iridaceae (2), and
Melanthiales (1).
Lilianae (7),
Cyclanthanae (1),
Pandananae (1), and
Velloziales (1).
Dioscoreales (2 of 3),
and Burmanniales (1).
Alismatanae (4),
Arecanae (4), and
Melanthiales (1).
Acorus calamus
Outgroup:
Dicotyledonous
Paleoherbs.

The maximum likelihood tree (79 spp., Fig. 1) and the resolved portions of the consensus tree produced by parsimony (122 spp., Fig. 3) are largely congruent with respect to the constituent species of the seven lineages listed above and the order of divergence of those lineages. Exceptions are: (1) Dioscoreales (excluding *Smilax glauca*) diverge earlier in the parsimony trees; (2) one species each of Cyclanthanae, Pandananae, and Velloziales make up an isolated clade in the maximum likelihood tree, which is found embedded within a clade of seven species of Lilianae in the parsimony tree; (3) *Burmannia biflora* is found in Asparagales in the maximum likelihood tree but with two species of Dioscoreales in the parsimony trees; and (4) *Aletris farinosa* occupies an isolated clade near the base of the maximum likelihood tree but is embedded within the clade of Asparagales in the parsimony trees. In both the maximum likelihood and parsimony trees, two species of Hypoxidaceae are included in Asparagales consistent with Dahlgren et al. (1985).

## Discussion

The order of divergence of the seven major lineages in our phylogenetic analyses is in general agreement with widely accepted views on the evolution of the monocotyledons. Recognition of the early divergences of Alismatanae (Cronquist, 1981; Dahlgren et al., 1985) and Dioscoreales (Dahlgren et al., 1985), and the affinities between the Alismatanae and the Aranae (Dahlgren et al., 1985; Grayum, 1991) correlate with the position of species from these superorders near the base of our molecular phylogenies. Postulated later divergences of Arecanae (Doyle, 1973), Bromelianae, Commelinanae, and Zingiberanae (Cronquist, 1981) are also consistent with our analyses.

In general, deep branches in the tree (Figs. 1, 4, and 5) are shorter than the terminal branches, indicating fewer nucleotide changes along the former. This relationship suggests either that the substitution rate during evolutionary radiations of the monocotyledons was unusually slow, that sampling bias occurred in part because of extinction events, or that the original radiations occurred rapidly. The fossil record, and especially that of fossil pollen, for angiosperms in general (Doyle & Hickey, 1976) and probably for the monocotyledons as well (Doyle, 1973) is certainly consistent with the hypothesis of rapid radiation.

*Acorus calamus* occupies a unique, basal position in all the trees generated for this study. Although *Acorus* was traditionally classified in Araceae because of superficial morphological similarities with the Australian aroid *Gymnostachys anceps*, aroid authorities have recently acknowledged long-recognized difficulties with this classification and, based on a substantial body of evidence (reviewed in Grayum, 1987), proposed removal of *Acorus* to a monogeneric family. A tree (not shown) constrained to include *Acorus* and four species of Arales as monophyletic that was analyzed over the subset of 79 species is 25 steps longer than the shortest trees. Our analysis thus indicates that removal of *Acorus* from the Araceae is consistent with a more parsimonious phylogenetic hypothesis and further offers an explanation for the failure to identify synapomorphies of this genus with other monocot species, if, as we suggest, *Acorus* is distinguished as the most basal extant lineage of monocotyledons.

Several other aspects of the tree of Figure 1, not already considered in the accompanying reports in this issue, are of interest. We have included *rbc*L sequences from 21 species in 12 of 30 families in the large order Asparagales (estimated 5,000 spp. or 10% of monocotyledons) sensu Dahlgren et al. (1985). These species are all found in a single monophyletic clade in both maximum likelihood and parsimony trees, together with only six other species: (1) *Aletris farinosa*, (Melanthiaceae); (2 and 3) two species of Iridaceae: *Anomatheca laxa* and *Iris* × *germanicum*; (4 and 5) two species of Orchidales: *Neuwiedia veratrifolia* (Apostasiaceae) and *Oncidium excavatum* (Orchidaceae); and (6) *Burmannia biflora*. Further, the clade of Asparagales (excluding Hypoxidaceae) is at least moderately supported by boot-

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Figure 3. Overview of the strict consensus of 109 equally parsimonious trees for 104 monocots and 18 dicots. These trees are of length 3,932, have consistency indices excluding uninformative characters of 0.267, and retention indices of 0.633. Note that the unresolved portions of this topology are within the terminal clades corresponding to: (1) Bromeliaceae; (2) that containing Commelinaceae and three species of Bromelianae; (3) Zingiberanae; (4) Asparagales; and (5) that consisting of Alismatanae, Arecanae, and one species of Melanthiales. The terminal species are identified in the Appendix in this issue and as genera in Figures 4 and 5. The number of species analyzed from each taxon is given parenthetically.

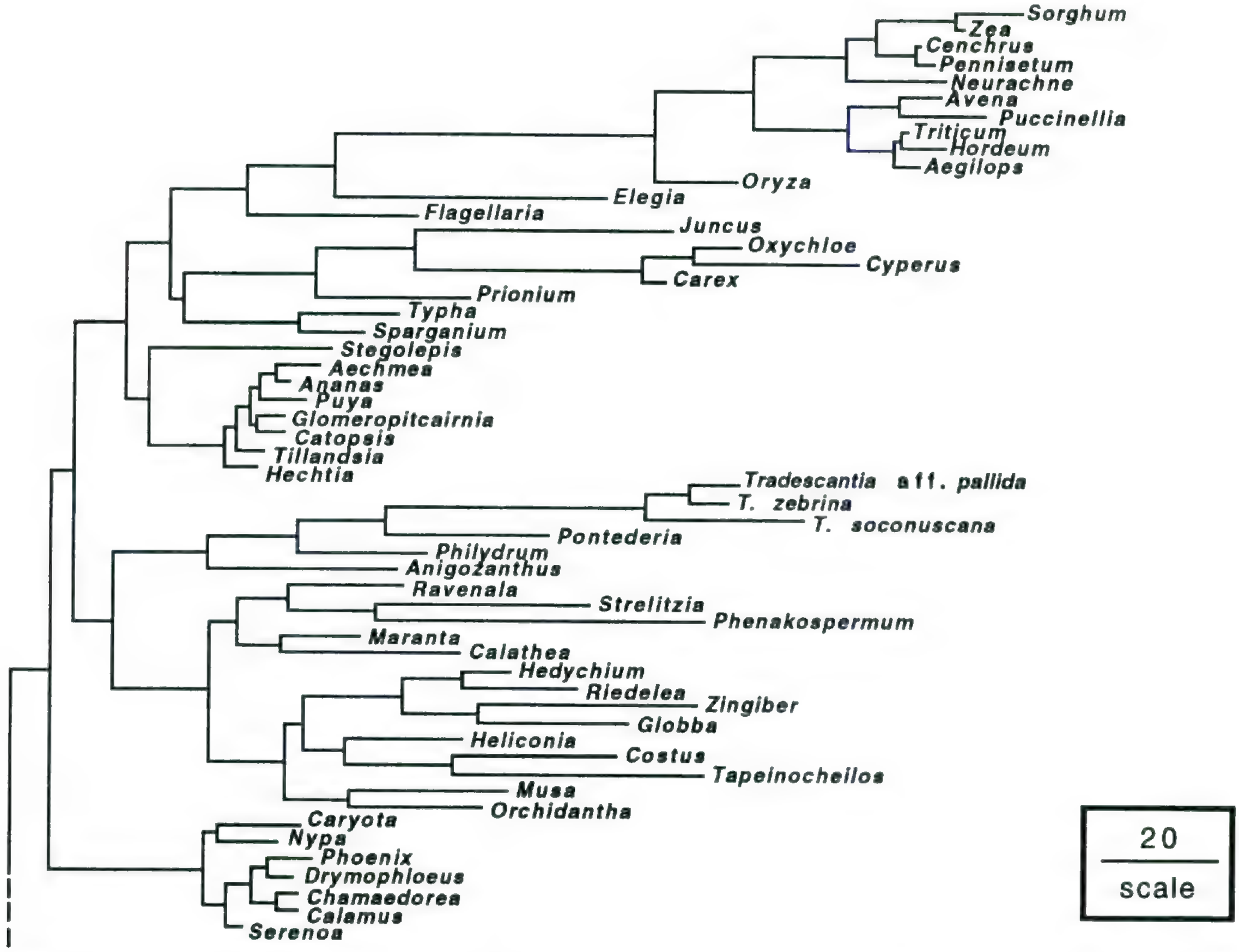


FIGURE 4. Terminal portion of one arbitrarily selected tree from the set of 109 trees (see consensus tree, Fig. 3) of length 3,932, consistency index of 0.267, and retention index of 0.633. This portion of the tree includes species of Commelinanae, Bromelianae, Zingiberanae, and Arecanae (see Fig. 5 for the remainder of the tree). Branch lengths correspond to the number of substitutions optimized along the branches. The scale bar is proportional to a branch length of 20 steps.

strap (84%) and decay (at least two steps longer) analyses. Duvall et al. (in review) have analyzed *rbc*L sequence data from four more species in three additional families of Asparagales that further support the common ancestry of this large order, and they note that the alliance between Iridaceae and Asparagales has morphological and anatomical support.

The historical treatment of Arecanae, Cyclanthanae, and Pandananae as at least marginally related taxa has been contradicted by subsequent taxonomic schemes that treat each as an unrelated superorder (Thorne, 1983) or as separate superorders with a loose alliance between Arecanae and Cyclanthanae (Dahlgren et al., 1985). Phylogenetic hypotheses based on the *rbc*L data support *Freycinetia* (Pandananae) and *Sphaeradenia* (Cyclanthanae) as sister species only distantly related to seven species of Arecanae. This arrangement suggests that Pandananae and Cyclanthanae are more ancient groups than Arecanae. Inclusion of *rbc*L data for a second species of Pandananae, *Pandanus veitchii* does not alter this result (Duvall et al., in review).

The *rbc*L trees suggest that *Smilax glauca* is allied with species of Liliales and isolated from the two other species of Dioscoreales (*Dioscorea polygonoides* and *Tacca integrifolia*). Among the three species a closer relationship has been proposed between the latter two, and *Smilax* has been placed outside of Dioscoreales because of a lack of similarities in secondary chemistry (Dahlgren et al., 1981). The more recent decision to place *Smilax* in Dioscoreales was based on "leaf morphology and floral appearance," although *Smilax* is hypothesized to form a "bridge" between Dioscoreales and species of Lilianae (Dahlgren et al., 1985).

Included in our analyses are 11 species of Poales and five species of the related Cyperales. Phylogenetic analyses of *rbc*L sequences of Poaceae

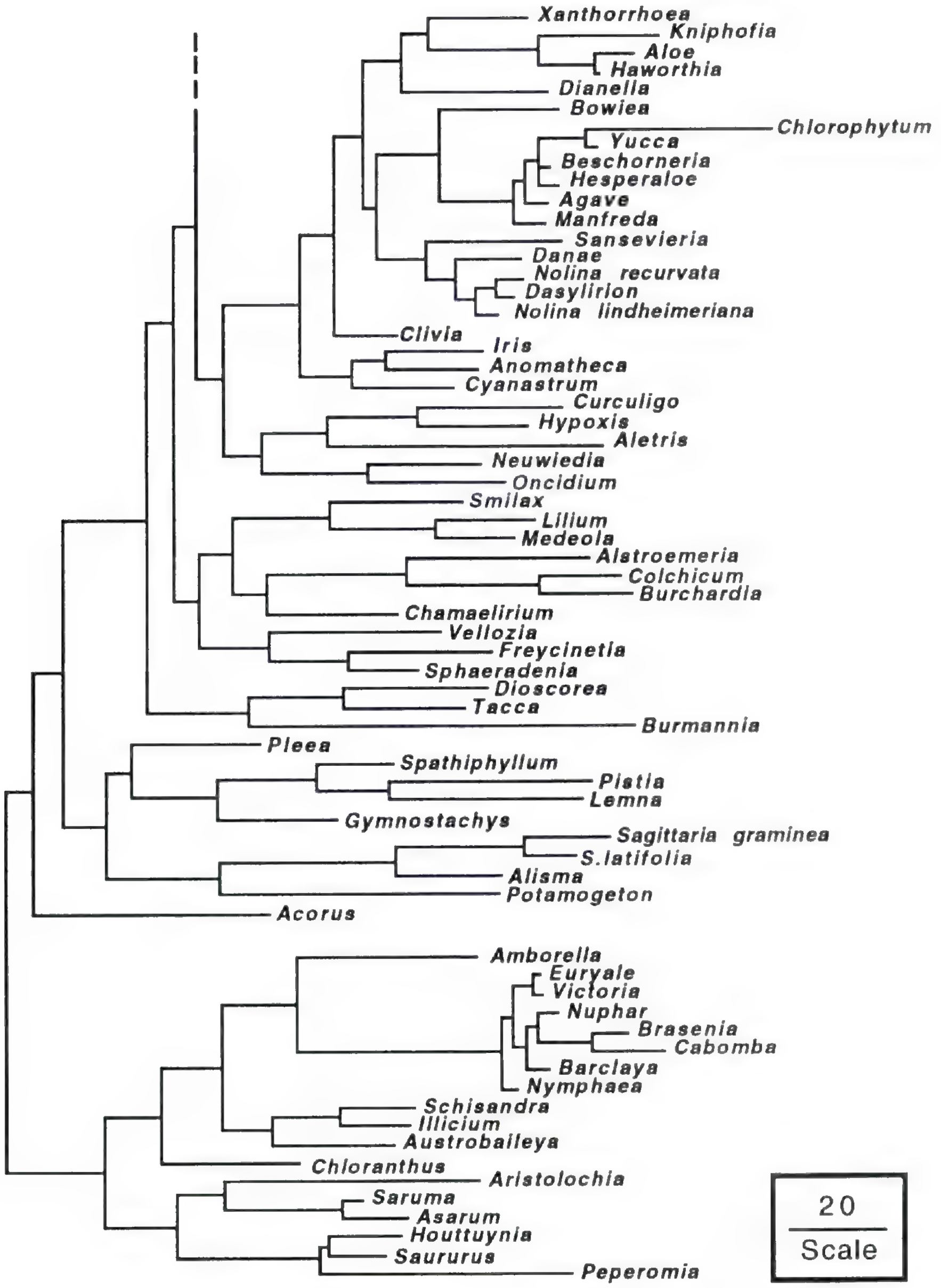


FIGURE 5. Remainder of the tree partially shown in Figure 4. This portion of the tree includes species of Aranae, Alismatanae, Lilianae, outgroup dicotyledons, and *Acorus calamus* (see Fig. 4 for the remainder of the tree). Branch lengths correspond to the number of substitutions optimized along the branches. The scale bar is proportional to a branch length of 20 steps.

have been thoroughly discussed (Doebley et al., 1990). We here note that pooid and panicoid grasses are segregated into sister clades in Figure 2, and that *Oryza sativa* occupies the most basal position of Poaceae. In the clade consisting of Poales (Fig. 3), a species of Restionaceae is most closely related to Poaceae, and Cyperales are found as a component of a sister clade which also contains Typhales contra Dahlgren et al. (1985). This topology is in agreement with the distribution of three inversions in the plastid genomes of these taxa (Doyle et al., 1992) that further predicts that Joinvilleaceae are immediately basal to Poaceae. This prediction has been confirmed by analysis of *rbc*L data as well (Duvall et al., in review).

In our analyses Commelinaceae (three species) cluster with three species of Bromelianae: *Pontederia sagittaria*, *Philydrum lanuginosum*, and *Anigozanthus flavidus* in a clade that is sister to Zingiberanae and separated from 18 other species

of Commelinanae (Fig. 4). A parsimony tree over the 79 species subset constrained to include 13 spp. of Commelinanae as monophyletic (not shown) is 15 steps longer than the tree without constraints. Parsimony analysis of *rbc*L thus does not support the recognition of a monophyletic Commelinanae.

*Pistia* has been tentatively aligned with *Lemna* based on similarities of seedling structure (Grayum, 1991). Analysis of *rbc*L sequences supports this alignment at a bootstrap value of 69% and a decay index value of at least two.

Three species of Melanthiaceae are found in three different primary lineages. These species exhibit a great deal of variation and when combined into a single family are considered a "difficult" treatment (Dahlgren et al., 1985). Our results support the suggestion (Dahlgren et al., 1985) that the Melanthiaceae should be divided into several families, and we further suggest that those families may not be closely related to each other.

The phylogenetic analysis presented here offers support for the recognition of seven primary lineages of monocotyledons that diverged over a relatively short period of geologic time. As noted, this result is in agreement with the taxonomic treatment of Dahlgren et al. (1985). However, a parsimony tree for the 79 species subset constrained to include nine of ten superorders sensu Dahlgren et al. (1985) as monophyletic groups (not shown) was considerably less parsimonious (52 steps longer). (Note that the tenth superorder, Triuridanae, is composed exclusively of achlorophyllous species unlikely to possess a phylogenetically meaningful copy of the *rbc*L sequence.) With regard to the paraphyletic arrangements of Bromelianae, Commelinanae, and Lilianae, the phylogenetic hypotheses presented here are at odds with those based on morphological, anatomical, chemical, and other characters. These discrepancies may reflect a new understanding of the affinities among these taxa. However, insufficient sampling of the *rbc*L data for these groups of species may also be a factor. For example, we have here included *rbc*L data from only half of the 52 families of Lilianae. Additional sampling of molecular characters may resolve these discrepancies or offer further insight into the phylogenetics of the monocotyledons.

The focus of this project was the phylogenetic framework supported by the *rbc*L data set for the monocotyledons. Another valuable feature of the data set, now generally available in GenBank, will be to further develop our understanding of the mechanisms and underlying probabilities of nucleotide substitution, particularly as influenced by structural and functional constraints of the molecules. These further studies will undoubtedly refine methods of the phylogenetic analysis of molecular data.

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# PHYLOGENETIC ANALYSIS OF THE ZINGIBERALES BASED ON *rbc*L SEQUENCES[1]

*James F. Smith,*[2,3,4] *W. John Kress,*[3] *and Elizabeth A. Zimmer*[2,3]

## Abstract

Morphological data have been used previously to construct phylogenies of the eight families of the Zingiberales, one of the most widely accepted monophyletic groups of flowering plants. To provide additional support for phylogenetic relationships within the order, and placement of the order among monocots, we present a parsimony analysis of DNA sequences from the chloroplast-encoded gene, *rbc*L, for 21 species of Zingiberales and proposed relatives. Five analyses with equal, and differential weights were performed. All analyses resulted in the same most parsimonious tree for taxa within the Zingiberales and the immediate outgroup. The closest sister group to the Zingiberales based on these data is a clade containing Commelinaceae/Haemodoraceae/Pontederiaceae. The tree topology within the order based on *rbc*L sequence data is different from previous morphological analyses. The order can be divided into two sister groups, one containing the Costaceae and Marantaceae, and the other, the remaining six families. All recognized families are monophyletic with the exception of the Musaceae, which is paraphyletic with the Cannaceae. With trees one and two steps longer than the most parsimonious trees, phylogenetic resolution is rapidly lost, suggesting that the phylogenetic utility of *rbc*L sequence data for the Zingiberales is limited to interordinal and intrafamilial relationships.

The Zingiberales, a morphologically distinctive order of monocots, are one of the most widely accepted monophyletic groups of plants (Bentham & Hooker, 1883; Petersen, 1889; Schumann, 1900, 1902, 1904; Hutchinson, 1934, 1959, 1973; Nakai, 1941; Tomlinson, 1962, 1969; Stebbins, 1974; Cronquist, 1978, 1981; Dahlgren & Rasmussen, 1983; Dahlgren et al., 1985; Kress, 1990). Dahlgren et al. (1985) listed six apomorphies for the Zingiberales: root hair cells shorter than other epidermal cells, sieve tube plastids containing starch, presence of silica bodies, epigynous flowers, lack of distinctive apertures on the pollen grains, and the occurrence of arillate seeds. In addition, the herbaceous arborescent stem, distichous phyllotaxy, large petiolate leaves with blades possessing transverse venation, conspicuous colorful bracteate inflorescences, and the substitution of one to five staminodia for the fertile stamens are characters easily used to identify members of the Zingiberales (Kress, 1990).

As currently classified, the order consists of eight families (Kress, 1990): Musaceae, Lowiaceae, Heliconiaceae, Strelitziaceae, Zingiberaceae, Costaceae, Marantaceae, and Cannaceae. Subordinal classification, including delimitation and rank of these families, has been subject to many changes (reviewed in Kress, 1990). Cladistic analyses of morphological characters have greatly improved the understanding of phylogenetic relationships of the families (Dahlgren & Rasmussen, 1983; Kress, 1990). Dahlgren & Rasmussen (1983) performed the first cladistic analysis of the Zingiberales using the eight families listed above and polarized characters using their Commeliniflorae. This analysis resulted in a single tree (Fig. 1) composed of three main clades that included the ginger group (Zingiberaceae/Costaceae and Marantaceae/Cannaceae), the banana group (Musaceae/Heliconiaceae), and the bird-of-paradise group (Strelitziaceae/Lowiaceae). The relationships among the three groups remained equivocal.

Kress (1990) re-analyzed the data of Dahlgren & Rasmussen (1983) and performed a separate analysis that included other characters which were rooted with the Bromeliales. This second analysis resulted in a different cladogram (Fig. 2) from that of Dahlgren & Rasmussen (1983). Although the ginger group relationship was retained in both, the families of the banana and bird-of-paradise groups

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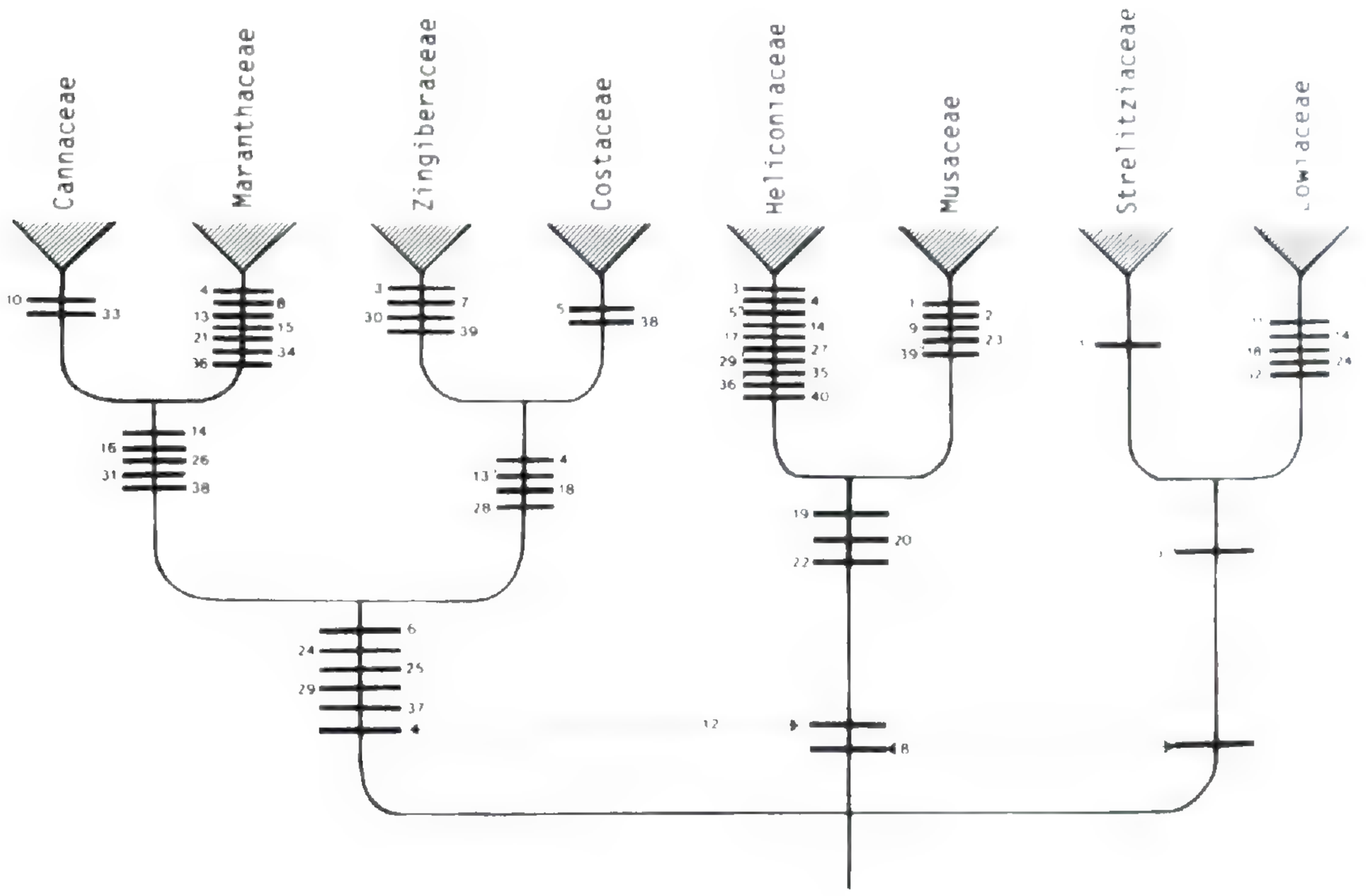



FIGURE 1. Cladogram of the Zingiberales from Dahlgren & Rasmussen (1983, their figure 9).

were shown to be paraphyletic (Kress, 1990). These analyses have been highly informative in terms of familial relationships, yet the utility of many of the morphological characters at this level is questionable. The eight families of the Zingiberales are highly distinctive with many unique and highly modified morphological structures. Interpretation of homology between families has posed difficult problems without detailed developmental analysis for many of the structures (Kirchoff, 1991).

The numerous autapomorphies of the Zingiberales have also made difficult the determination of the evolutionary relationship of the order to other monocots. The Zingiberales have generally been allied with the Bromeliales and/or Commelinales (Hutchinson, 1973; Dahlgren et al., 1985; Thorne, 1992). The presence of starchy endosperm, epicuticular wax of the *Strelitzia* type, UV-fluorescent organic acids in the cell walls, and two or four subsidiary cells in the stomatal complex are all specialized characters that unite the Zingiberiflorae with the Bromeliiflorae and Commeliniflorae (Dahlgren et al., 1985). Most modern classifications have placed the Zingiberales near the Bromeliales (containing the single family Bromeliaceae) (Hutchinson, 1973; Stebbins, 1974; Takhtajan, 1980; Cronquist, 1978, 1981) based on the similarity of inflorescence and flower structures (primarily the large, conspicuous bracts and petaloid perianth parts). Although these morphological homologies are potentially equivocal, the presence of several chemical constituents (myricetin and/or quercetin glycosides) also has suggested a common ancestor for the Zingiberales and Bromeliales (Williams & Harborne, 1977). Thorne (1992), however, recognized three separate orders in his superorder Commelinanae: Bromeliales, Commelinales, and Zingiberales.

Alternatively, Walker (1987) derived his Zingiberidae (excluding the Bromeliales) and his Pontederiidae (Haemodoraceae, Pontederiaceae, and Philydraceae) directly from a liliid lineage. Sepal nectaries, vessels primarily in the roots, and several chemical characters (e.g., chelidonic acid) found in the Zingiberales support their placement with a lilialean lineage (Takhtajan, 1980).

The use of molecular characters in cladistic analyses has been highly successful in plants (Palmer et al., 1988; Crawford, 1990), particularly in taxonomically difficult groups in which it is hard to interpret morphological homology (e.g., Chase & Palmer, 1989; Smith, 1991). Recently, sequence data derived from the chloroplast gene *rbc*L, which encodes the large subunit of ribulose bisphosphate carboxylase, has provided resolution at higher taxonomic levels in plants (e.g., Doebley et al., 1990; Donoghue et al., 1992; Olmstead et al., 1992; other papers this issue). The relatively slow rate of mutation of the *rbc*L gene has made this gene useful for taxonomic investigations at and above the generic level. However, the limits and taxonomic range for which *rbc*L can adequately resolve phylogenetic relationships have not been examined widely.

To compare phylogenies based on morphological analyses in the Zingiberales, we initiated a cladistic analysis of *rbc*L sequence data. Our goals in this research were: (1) to examine the monophyly of

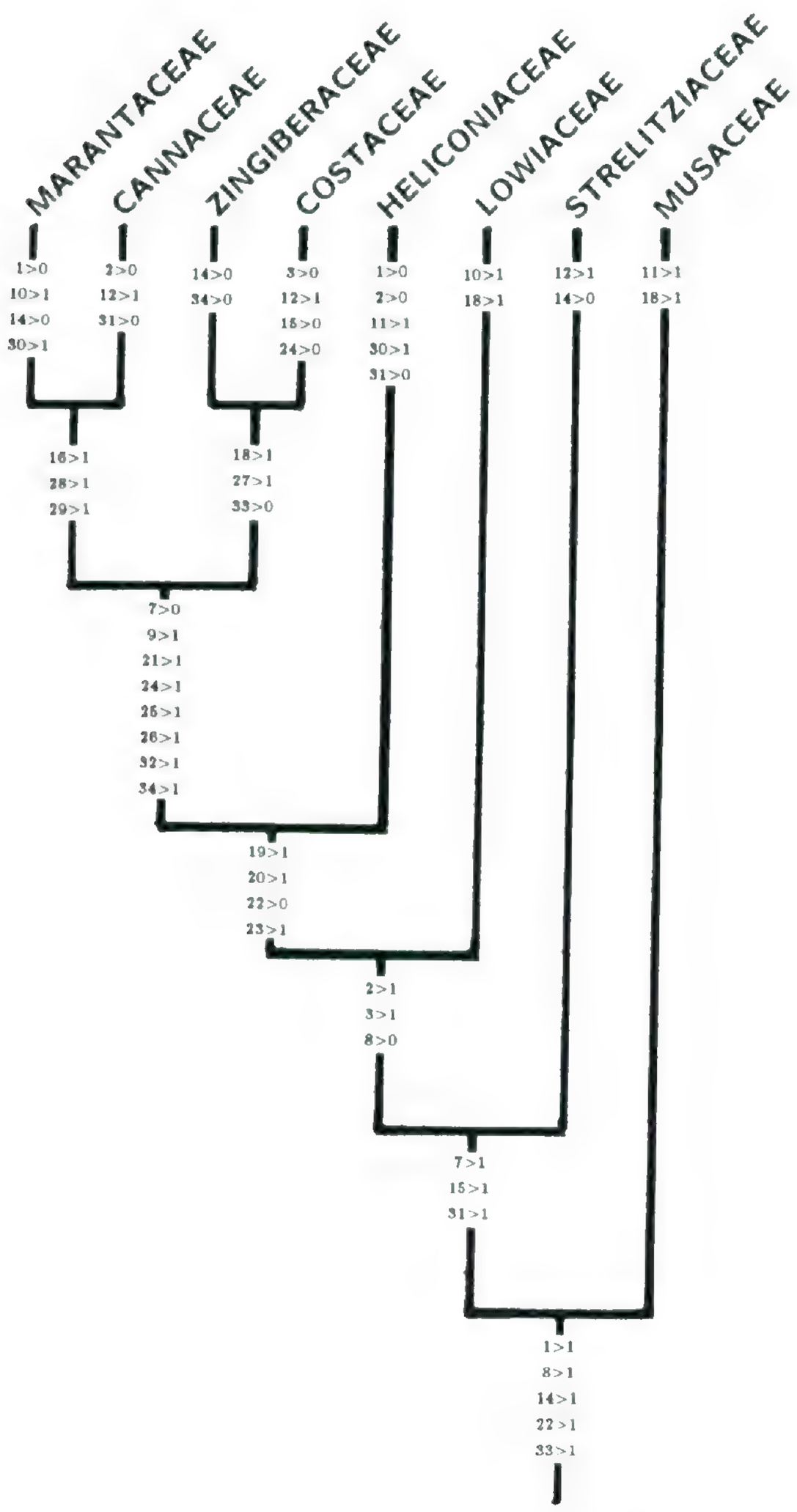



FIGURE 2. Most parsimonious tree of the Zingiberales from Kress (1990, his figure 7).

the eight recognized families; (2) to construct the phylogenetic relationships of the families within the order based on *rbc*L sequence data; and (3) to determine the sister group relationship of the Zingiberales.

## MATERIALS AND METHODS

Species were selected in an attempt to represent the most divergent members of each family. For example, in the large family Zingiberaceae, the species selected represent each of the four tribes. Different genera were represented wherever possible, depending on availability and number of genera in each family. A minimum of two taxa per family was chosen to reduce potential long branch effects (Felsenstein, 1978), which result when a single taxon with no close affinities is included in an analysis. Species, collection localities, and voucher information are listed in Table 1.

Total genomic DNA was extracted from fresh or frozen leaf tissue by a modified CTAB method (Smith et al., 1991 [1992]). An approximately 1,401 bp segment of double-stranded DNA containing the sequence for the *rbc*L gene was amplified via the Polymerase Chain Reaction (Cetus Corporation) (PCR). Two synthetic oligonucleotides were used as amplification primers. The 5′ primer is the Z-1 *rbc*L primer based on the first 30 bp of the *rbc*L sequence of maize, and the 3′ primer is the corresponding Z-1375R primer, which is a 26 bp primer derived from position 1375–1401 of the maize sequence (Zurawski, DNAX). Initial attempts were made to amplify DNA from zingiberalean taxa using the primers of Olmstead et al. (1992); however, an apparent substitution unique to the Zingiberales in this region of the gene prevented amplification with these primers. This substitution is currently under investigation (Smith et al., unpublished).

Sequences were obtained by cloning the PCR product into BlueScript SK$^+$ (Stratagene, Inc.) using either the *Hinc II* or *EcoR V* site. The ligation was facilitated by first incubating the PCR products with DNA polymerase to assure blunt ends. The products of the ligation reactions were used to transform competent cells of *Eschericia coli* (XL-1 Blues; Stratagene, Inc.). Actively growing liquid cultures of transformed bacteria were inoculated with the helper phage VCS-M13 (Stratagene, Inc.) and single-stranded DNA was harvested that contained the inserted *rbc*L gene. This single-stranded DNA was then sequenced using Sequenase version 2.0 (US Biochemicals), and fragments were separated on 4% polyacrylamide gels. Internal sequencing primers were derived from sequences distributed by G. Zurawski (DNAX).

Additional sequences for *Lilium*, *Magnolia*, *Vellozia*, *Puya*, *Tillandsia*, *Stegolepis*, *Pontederia*, *Lachnanthes*, *Tradescantia*, and *Maranta* were graciously provided by colleagues (see Chase et al., 1993).

Sequences were read directly from the autoradiographs and entered into a NEXUS file. This file was read into PAUP version 3.0s (Swofford, 1991) for cladistic analysis. Characters were directly scored for each nucleotide and not modified in any way. Missing data or ambiguous regions were scored as missing. Initial analyses used HEURISTIC SEARCH and STEPWISE ADDITION of 500 RANDOM ADDITION SEQUENCE replicates, TBR branch swapping, saving ALL MINIMAL

TREES, and COLLAPSING ZERO LENGTH BRANCHES. These options were chosen as an initial analysis due to the sensitivity of PAUP (and all other programs) to taxon order in the data matrix (Maddison, 1991). The order of taxa in the data set was then altered to produce the same most parsimonious tree with the GENERAL HEURISTIC OPTION and default options for further weighting analyses. Neighborhood trees of 1 and 2 steps longer were also examined using the same default options with the exception that trees of a specified length and shorter were saved.

Several separate analyses were performed using the above options to determine if choice of outgroup had an effect on the arrangement of taxa within the Zingiberales. These analyses used: (1) *Magnolia* as the outgroup, with all other monocots included as ingroup; (2) *Lilium* as the outgroup with all other monocots included as ingroup, and *Magnolia* excluded; (3) *Tradescantia Pontederia–Lachnanthes* as outgroup, with only the zingiberalean taxa included as ingroup.

Character state changes were plotted onto trees using the ACCTRAN option. Because the DELTRAN option can sometimes drastically alter the distribution when equally parsimonious options are available, character state changes also were plotted with this option, and the two distributions compared.

## Results

### SEQUENCE DATA

Sequences of 1,345 bp or more were obtained for 33 species including 10 sequences graciously provided by other workers (see Chase et al., 1993) (Table 1). For the 32 species used in the majority of analyses (excluding *Magnolia*, which was used to determine outgroup relationships), 464 positions (~34%) were variable. Of these 464 characters, 183 (~39% of the variable characters) were autapomorphic. Therefore, 281 of the original 1,345 bp (~21%) were shared by two or more taxa. Of the 464 variable characters, 105 (~23%) were first codon positions, 92 (~20%) were second positions, and 267 (~57%) were third positions (Table 2).

### ANALYSES

The equally weighted analysis from the RANDOM ADDITION SEQUENCE search resulted in two most parsimonious trees of 1,163 steps (CI of 0.41; RI of 0.49). The two trees differed only in the relationships of *Stegolepis* and the Bromeliaceae. The strict consensus of these most parsimonious trees is presented in Figure 3. The topology was unaltered whether *Magnolia*, *Lilium*, or *Tradescantia/Lachnanthes/Pontederia* were used to root the tree.

Character state change distributions differed only slightly between the ACCTRAN and DELTRAN option. At only four nodes did the distributions differ in more than two character state changes and in none of these did a strongly supported node become weakly supported or vice versa. Based on the character state distribution of the most parsimonious trees, 709 (~61%) of the 1,163 character state changes were transitions, and 454 (~39%) were transversions (Table 3).

The strict consensus of the 62 trees of 1,164 steps or fewer loses most of the resolution found in the most parsimonious trees (Figs. 3, 4). A search for trees two steps longer than the most parsimonious trees produced 1,541 trees of 1,165 steps or fewer. A strict consensus of these 1,541 trees lost nearly all resolution with the exception of monophyly of the five major clades in the Zingiberales, Strelitziaceae, Zingiberaceae, Cannaceae, Lowiaceae, and *Calathea/Marantochloa*, as well as outgroup clades (Fig. 4).

## Discussion

A cladistic analysis of the *rbc*L sequence data produced a single most parsimonious tree for the families of the Zingiberales (Fig. 3) that differs from any previous phylogenetic analysis of morphological data (Figs. 1, 2) (Kress, 1990). The Lowiaceae and Strelitziaceae lineage is the only between-family clade shared by both the molecular analysis and one of the cladistic analyses of morphological characters (Dahlgren & Rasmussen, 1985) (Fig. 1).

The conflicts between the trees based on morphological characters and molecular data are many. One conspicuous example pertains to floral morphology. In all traditional classifications of the order (see Kress, 1990, for summary), the reduction in the number of pollen-bearing stamens from 6 or 5 (Musaceae, Strelitziaceae, Lowiaceae, and Heliconiaceae) to 1 or $\frac{1}{2}$ (Zingiberaceae, Costaceae, Cannaceae, and Marantaceae), and the associated modification of these stamens into petaloid staminodes, are characters that have served as the basis for dividing the families into two basic groups, the banana group and the ginger group, respectively. The homology of these specialized floral features

TABLE 1. Sources of *rbc*L sequences (all material is deposited at US, SEL, or DUKE). Voucher and Genbank information for sequences obtained from other laboratories is referenced in the appendix to this volume.

| Species | Voucher | Source | Genbank # |
|---|---|---|---|
| Bromeliaceae | | | |
| *Tillandsia elizabethae* | | D. Clark | |
| *Puya dyckioides* | | D. Clark | |
| Rapateaceae | | | |
| *Stegolepis allenii* | | D. Clark | |
| Commelinaceae | | | |
| *Tradescantia soconuscana* Matuda | Faden 76-98 | Mexico | L05463 |
| *Tradescantia* sp. | | M. Duvall | |
| Pontederiaceae | | | |
| *Pontederia* | | D. Clark | |
| Haemodoraceae | | | |
| *Lachnanthes* | | M. Chase | |
| Velloziaceae | | | |
| *Vellozia* | | D. Clark | |
| Liliaceae | | | |
| *Lilium superbum* | | M. Chase | |
| Typhaceae | | | |
| *Typha latifolia* L. | Kress 90-3170 | Maryland, USA | L05464 |
| *Typha latifolia* L. | | M. Duvall | |
| Cannaceae | | | |
| *Canna indica* L. | Kress 80-1124 | Indonesia | L05445 |
| *Canna tuerkheimii* Kranzlin | Kress 76-653 | Panama | L05446 |
| Costaceae | | | |
| *Costus barbatus* Suess. | SEL 86-0550 | Marie Selby Botanical Gardens, Sarasota, Florida | L05447 |
| *Tapeinochilos ananassae* K. Schum. | Kress 79-1114 | Duke University, Durham, North Carolina | L05462 |
| *Monocostus uniflorus* (Poepp. ex Petersen) Maas | Kress 79-1112 | Peru | L05454 |
| Heliconiaceae | | | |
| *Heliconia latispatha* Benth. | SEL 80-1610 | Marie Selby Botanical Gardens, Sarasota, Florida | L05451 |
| *Heliconia paka* A. C. Smith | Kress 79-1072 | Fiji | L05452 |
| Lowiaceae | | | |
| *Orchidantha fimbriata* Holttum | Kress & Beach 87-2159 | Malaysia | L05456 |
| *Orchidantha siamensis* K. Larsen | Kress 92-3468 | Malaysia | L05457 |
| Marantaceae | | | |
| *Maranta leuconeura* | | M. Duvall | |
| *Calathea loeseneri* Macbride | SEL 85-31 | US Botanic Garden, Washington, D.C. | L05444 |
| *Marantochloa purpurea* (Ridley) Milne-Redhead | Kress 78-894 | Wilson Botanical Garden, Costa Rica | L05453 |
| Musaceae | | | |
| *Ensete ventricosum* (Welw.) Cheesman | s.n. | Wilson Botanical Garden, Costa Rica | L05448 |

TABLE 1. Continued.

| Species | Voucher | Source | Genbank # |
|---|---|---|---|
| *Musa acuminata* Colla | s.n. | US Botanic Garden, Washington, D.C. | L05455 |
| Strelitziaceae | | | |
| *Phenakospermum guianensis* (L. Richt.) Miq. | Kress 86-2099 | French Guiana | L05458 |
| *Ravenala madagascariensis* J. F. Gmel. | Kress 92-3504 | US Botanic Garden, Washington, D.C. | L05459 |
| *Strelitzia nicolai* Regel & Koch | Kress 91-3169 | US Botanic Garden, Washington, D.C. | L05461 |
| Zingiberaceae | | | |
| *Globba curtisii* Holttum | Kress & Beach 87-2161 | Malaysia | L05449 |
| *Hedychium flavum* Roxb. | USBG 90-653 | US Botanic Garden, Washington, D.C. | L05450 |
| *Riedelea* aff. *wrayii* | SEL 83-203 | Lyon Arboretum, Honolulu, Hawaii | L05460 |
| *Zingiber gramineum* Noronha | Kress 91-3266 | Lyon Arboretum, Honolulu, Hawaii | L05465 |

is supported by ontogenetic studies in the Zingiberales as well (Kirchoff, 1983, 1988, 1991). Although the four families of the banana group may be variously related, the ginger group, defined by these highly derived staminal features, has always been considered monophyletic (Dahlgren & Rasmussen, 1985; Kress, 1990; Kirchoff, 1991).

The topology based on the molecular data places the four families of the ginger group into three separate lineages (Marantaceae and Costaceae; Cannaceae and Musaceae; and Zingiberaceae and Heliconiaceae; see Fig. 3), which would require at the minimum three independent reductions (if 5–6 stamens is plesiomorphic) or one increase and two reversals to reduction (if $1-\frac{1}{2}$ stamens is plesiomorphic) in stamen number. Although we should certainly reconsider the possible nonhomology of these traditionally recognized morphological features, the molecular characters must be examined critically (through increased sampling of taxa, or examination of other molecular characters) before concluding that the morphological features are homoplastic.

The rapid "decay" of the various clades in the most parsimonious tree found from the *rbc*L data suggests that the interfamilial phylogenetic signal of this plastid gene is low for the Zingiberales (Fig. 4). There are 62 different topologies that are one step or fewer longer than the most parsimonious; 1,541 topologies can be found searching for trees two or fewer steps longer.

In contrast to interfamilial relationships, the *rbc*L data strongly support both the monophyly of the order within the monocots as well as the monophyly of most of the families. Although the position of the *Lachnanthes/Pontederia/Tradescantia* clade as the sister group to the Zingiberales collapses in the consensus of trees one step longer (Fig. 3), the coherence of the order itself remains robust. In a larger analysis of the phylogeny of the monocots

TABLE 2. Variable characters according to codon position. Homoplastic character states are based on the ACCTRAN character state distributions for the most parsimonious trees (Fig. 3). The first values are the numbers of characters, the second are the percentages of total states. Synapomorphic character states include only non-homoplastic character states.

| Position | Variable | | Homoplastic | | Synapomorphic | | Autapomorphic | |
|---|---|---|---|---|---|---|---|---|
| First | 105 | ~ 22% | 30 | ~ 15% | 23 | ~ 28% | 52 | ~ 28% |
| Second | 92 | ~ 20% | 30 | ~ 15% | 19 | ~ 23% | 43 | ~ 23% |
| Third | 267 | ~ 58% | 139 | ~ 70% | 40 | ~ 49% | 88 | ~ 49% |
| Total | 464 | 100% | 199 | 100% | 82 | 100% | 183 | 100% |

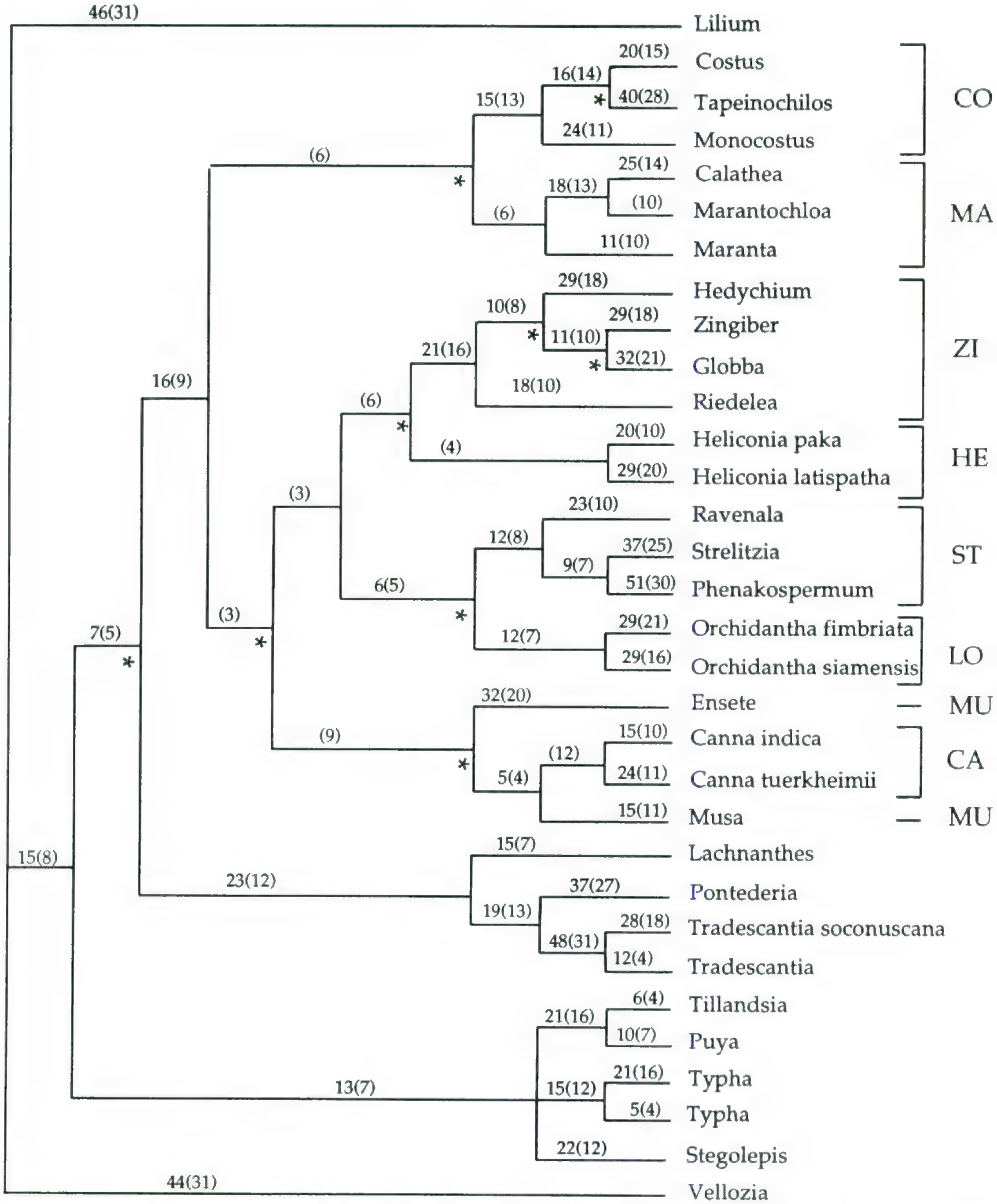
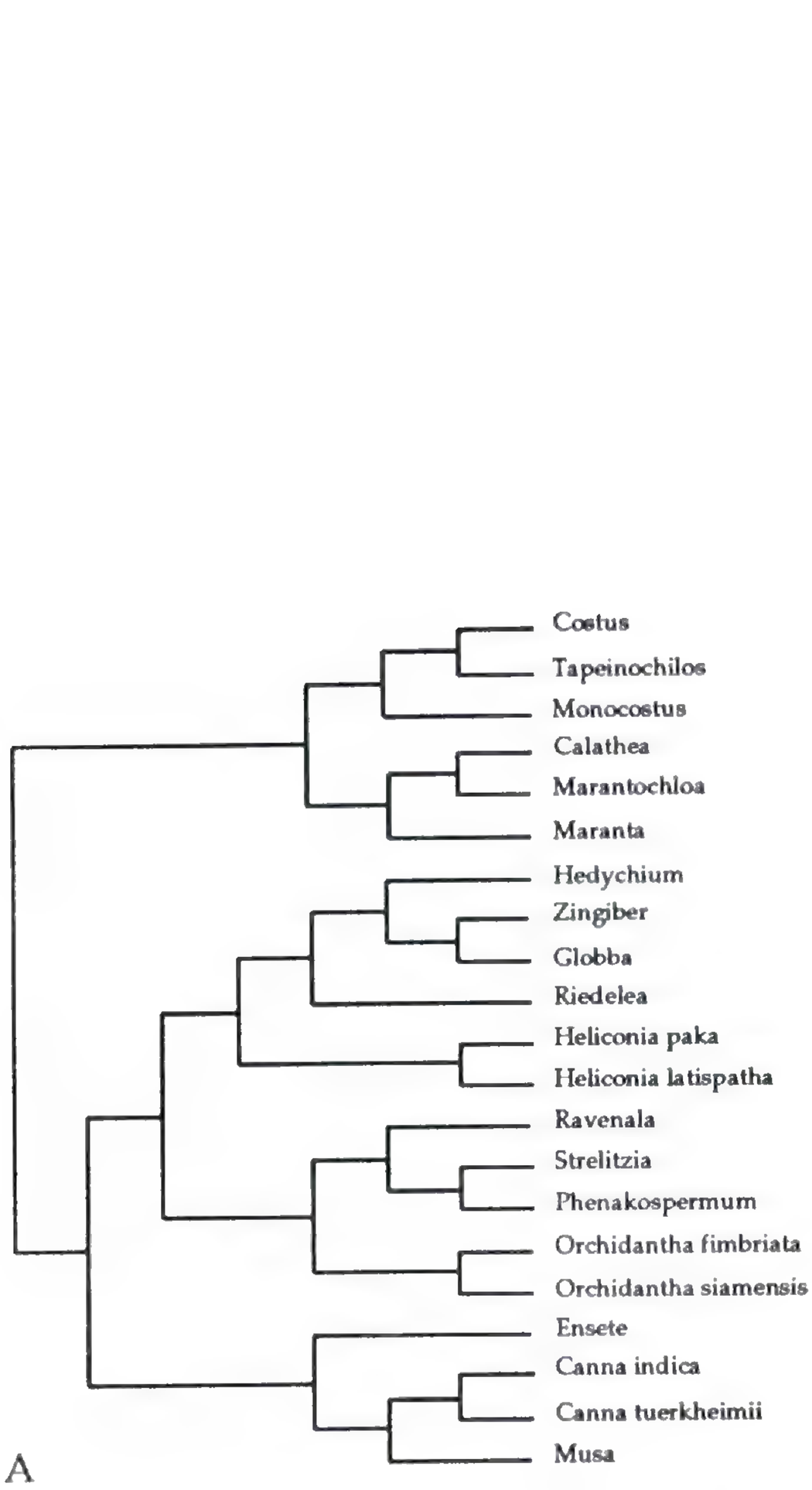
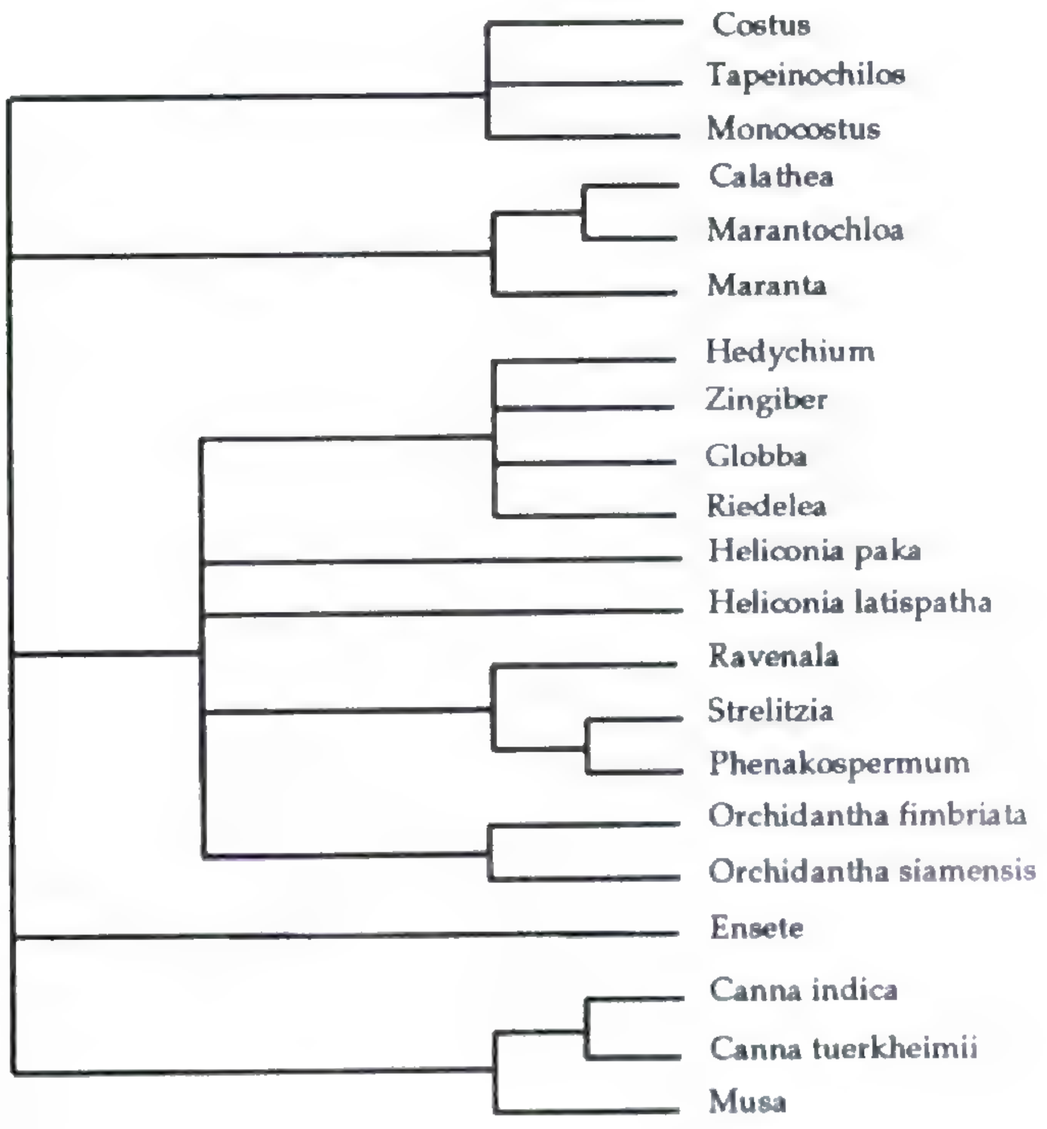



FIGURE 3. Strict consensus of the two most parsimonious trees from the equally weighted analysis. The two trees differ only in the relationships of *Stegolepis*/*Typha*/Bromeliaceae. Numbers along branches indicate substitutions supporting that clade, numbers in parentheses are the portion of substitutions that are homoplastic. Character state change distributions are based on tree 1 of the two most parsimonious trees (*Typha* as sister group to Bromeliaceae), and the ACCTRAN option. Asterisks denote clades that are lost in the consensus of the 62 trees one step longer than the most parsimonious trees (see Fig. 4). Families of the Zingiberales are denoted as follows: CO = Costaceae, MA = Marantaceae, ZI = Zingiberaceae, HE = Heliconiaceae, ST = Strelitziaceae, LO = Lowiaceae, MU = Musaceae, CA = Cannaceae.



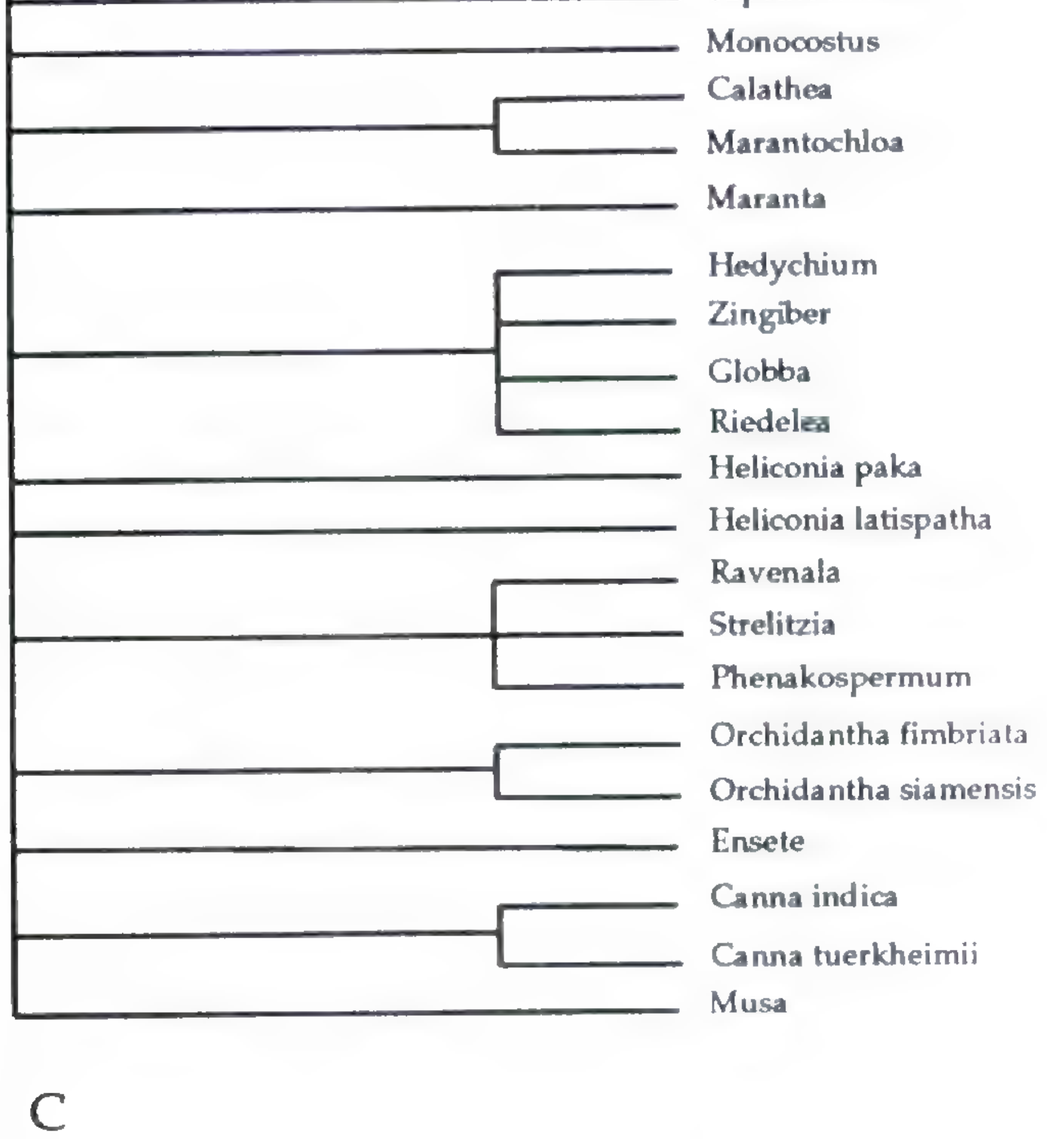




FIGURE 4. Strict consensus trees of the topologies based on A: two trees of 1,163 steps each, B: 62 trees of 1,164 steps each, and C: 1,541 trees of 1,165 steps each. Only taxa of the Zingiberales are illustrated in these figures.

based on *rbc*L sequence data (Duvall et al., 1993), the sister group relationships of the Zingiberales and the Haemodoraceae/Pontederiaceae/Commelinaceae is supported.

The Musaceae (paraphyletic with the Cannaceae) are the only family in the Zingiberales that is not monophyletic in the most parsimonious tree. The monophyly of the Heliconiaceae is also lost in

TABLE 3. Type of character state changes based on tree 1 of the most parsimonious trees (*Typha* and Bromeliaceae as sister groups) in the equally weighted analysis (Fig. 3). Transversions are indicated in bold.

| | A | C | G | T |
|---|---|---|---|---|
| A | — | **103** | 276 | **110** |
| C | — | — | **137** | 433 |
| G | — | — | — | **104** |

the consensus of trees one step longer. These discrepancies may be the result of limited sampling. Sequences for additional *Heliconia* and *Canna* species, as well as other representatives of the Musaceae, may stabilize these portions of the tree. The other six families are well supported as monophyletic groups by the molecular data even in the less parsimonious trees.

A clear weakness in this analysis is the unbalanced sampling for some of the families, e.g., Heliconiaceae and Musaceae. The addition of two to three more taxa for these families may result in a more robust analysis and provide a better overall estimate of phylogeny for the Zingiberales. In particular, the monophyly of these families would probably be more strongly supported by the addition of taxa to the analysis.

Regardless of the problem of uneven taxon sampling, the limitations of the data set are most apparent when the distribution of character state changes are mapped onto the tree (Fig. 3). Of the 281 phylogenetically informative characters used in the analysis, there are only 90 (32%) synapomorphic character state changes that are not homoplastic (based on Fig. 3). Within the Zingiberales, there is only one character state change that is synapomorphic between families and not homoplastic (Strelitziaceae and Lowiaceae lineage). In contrast, seven nonhomoplastic character state changes support the monophyly of the order, and 29 nonhomoplastic character state changes support monophyly of, or are synapomorphic within, the families of the Zingiberales. Likewise, the monophyly of the outgroup clades (Haemodoraceae/Pontederiaceae/Commelinaceae and Bromeliaceae/Typhaceae/Rapateaceae) is supported by nonhomoplastic character states (Fig. 3).

The weakness of the signal is also apparent when codon position is examined. Third position codons account for 58% of the variation in the data set and 70% of the homoplasy (Table 2). This is not a surprising result as the redundancy of the genetic code permits a higher rate of substitution at third position codons without altering the amino acid sequence of the resulting protein. However, the high percentage of homoplastic third position codons (139 of the 464 variable positions) and the presence of 3–4 different nucleotides at 64 of these sites indicate that the substitution rate within the Zingiberales may be close to saturation, thereby reducing the interpretable phylogenetic signal of the *rbc*L sequence data.

Our results suggest that although phylogenetic signal is present in the data, there is a "window" in which *rbc*L sequence data does not strongly resolve phylogenetic relationships. For the Zingiberales this window is at the between-family level. At the ordinal and family levels, the molecular data are much more robust in defining and resolving phylogenetic relationships.

An explanation for this window may be related to the age of the Zingiberales and the time since divergence of the families within the order. Olmstead et al. (1992) explained the lack of phylogenetic resolution of the higher dicot lineages as a result of rapid divergence of these clades during the late Cretaceous. In contrast, phylogenetic resolution of lineages within the Asteridae sensu lato is resolved adequately with *rbc*L sequence data (Olmstead et al., 1992).

Extant Zingiberales possess numerous derived morphological features, and five of the eight families are known from the fossil record (Kress, 1990). Although most of the fossil material has been collected in Eocene deposits, the oldest specimens are leaves of the Zingiberaceae from the late Cretaceous (Hickey & Peterson, 1978). The common ancestor of the lineages leading to the banana group is therefore hypothesized to have diverged from the remainder of the Zingiberales by the late Cretaceous (Friedrich, 1987), suggesting that the major lineages within the order had rapidly differentiated by the early Tertiary. These times of lineage splitting and divergence in the Zingiberales are similar to those described by Olmstead et al. (1992) for the higher dicots. The lack of phylogenetic resolution using *rbc*L data in these unrelated flowering plant taxa may be due to their common age of origin and diversification.

To further clarify phylogenetic relationships within the Zingiberales, data from other sources will be necessary. The morphological data will necessarily be re-examined to accommodate new interpretations of homology and to include taxa such that the molecular and morphological data sets will be directly comparable. Sequence data from the nuclear encoded 18S and 26S ribosomal genes are currently being collected for the Zingiberales (Kress et al., unpublished results), which have been suc-

cessful in resolving some ancient phylogenetic events in other seed plants (Hamby & Zimmer, 1992). Additional data may also be obtained by restriction site comparison of the highly conserved inverted repeat regions of the chloroplast genome (Downie & Palmer, 1992; Smith et al., unpublished results).

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# PHYLOGENETIC RELATIONSHIPS AMONG MEMBERS OF SAXIFRAGACEAE SENSU LATO BASED ON *rbc*L SEQUENCE DATA[1]

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## ABSTRACT

In an attempt to elucidate relationships among the morphologically diverse members of Saxifragaceae sensu lato, phylogenetic analyses of *rbc*L sequence data were conducted on representative genera of 16 of the 17 subfamilies. Also included were many putatively related families, as well as a diverse array of dicotyledonous flowering plants. Our phylogenetic analyses suggest that taxa of Saxifragaceae sensu lato are allied with at least 10 separate, often distantly related, lineages of several subclasses of flowering plants. Sequence data, in combination with other lines of evidence, suggest that Saxifragaceae sensu stricto should consist only of subfamily Saxifragoideae, a group of about 30 herbaceous genera that form the core of Saxifragaceae sensu lato. These data also suggest that potential close relatives of Saxifragaceae sensu stricto include Iteoideae, Pterostemonoideae, and Ribesoideae and possibly Penthoroideae and Tetracarpaeoideae, all traditional subfamilies of Saxifragaceae sensu lato, as well as Crassulaceae. These members of Saxifragaceae sensu lato, along with Saxifragaceae sensu stricto, Crassulaceae, and several genera from the subclass Hamamelidae, are basal to a large assemblage of taxa, most of which are usually placed in Rosidae. Within this primarily rosid alliance, representatives of four other subfamilies of Saxifragaceae sensu lato (Francooideae, Baueroideae, Parnassioideae, and Lepuropetaloideae) are allied with the rosid families Greyiaceae, Cunoniaceae, and Celastraceae. According to *rbc*L sequence evidence, Hydrangeoideae and Cornaceae are closely related members of a clade that is basal to a large group of taxa primarily from subclass Asteridae. Representative genera of four subfamilies of Saxifragaceae sensu lato (Phyllonomoideae, Escallonioideae, Montinioideae, and Vahlioideae) are in our results allied with taxa usually included in Asteridae. Significantly, relationships of Saxifragaceae sensu lato suggested by *rbc*L sequence data are in very close agreement with those supported by several other lines of evidence, especially embryology, serology, and iridoid chemistry.

Many systematists consider Saxifragaceae to occupy a pivotal position in the evolution of a number of major angiosperm lineages. Takhtajan (1969, 1980), for example, described such diverse groups as Myrtales, Cornales, Celastrales, Gentianales, and Campanulales as all having been derived from an ancestral "Saxifragalean stock." In spite of its potential evolutionary importance, however, Saxifragaceae are one of the least understood families of flowering plants. The family has been thought to consist of a wide array of morphologically diverse taxa, and the heterogeneity among the proposed constituents of Saxifragaceae is so great that the family has been nearly impossible to define. As a result, few families of angiosperms offer the magnitude and diversity of systematic problems posed by Saxifragaceae.

Many different classifications of Saxifragaceae have been proposed; a partial listing includes Cronquist (1981), Dahlgren (1975a, 1980, 1983), Dahlgren et al. (1981), Engler (1890, 1928), Hutchinson (1973), Schulze-Menz (1964), Takhtajan (1969, 1980, 1987), and Thorne (1968, 1976, 1983, 1992). These schemes of classification differ from one another not only in how they define Saxifragaceae, but also in how they ally them with other families. Frequently, the differences among classifications of Saxifragaceae are substantial.

A comparison of six recent classifications of the family is shown in Table 1. Saxifragaceae were broadly defined by Engler (1890, 1928) and Schulze-Menz (1964). The Saxifragaceae of Schulze-Menz (1964) are the most broadly de-

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TABLE 1. Comparison of six classifications of Saxifragaceae, in relation to that of Schulze-Menz (1964), or Saxifragaceae sensu lato. Numbers in parentheses indicate the number of genera in each of the 17 subfamilies of Saxifragaceae sensu lato. Subfamilies of Saxifragaceae sensu lato are listed in parentheses under the taxa in which they are placed in the other five classifications.

| Schulze-Menz (1964) | Hutchinson (1973) | Thorne (1992) | Cronquist (1981) | Dahlgren (1983) | Takhtajan (1987) |
|---|---|---|---|---|---|
| Archichlamydeae | Herbaceae | Rosanae | Rosidae | Rosiflorae | Rosidae–Rosanae |
| Rosales | Saxifragales | Saxifragales | Rosales | Saxifragales | Saxifragales |
| Saxifragaceae | Saxifragaceae (Saxifragoideae, Lepuropetaloideae) | Saxifragaceae (Saxifragoideae) | Saxifragaceae (Saxifragoideae, Penthoroideae, Francooideae, Parnassioideae, Lepuropetaloideae, Vahlioideae, Eremosynoideae) | Saxifragaceae (Saxifragoideae, Penthoroideae, Francooideae, Vahlioideae) | Saxifragaceae (Saxifragoideae) |
| Saxifragoideae (30) | Crassulaceae (Penthoroideae) | Tetracarpaeaceae (Tetracarpaeoideae) | Hydrangeaceae (Hydrangeoideae) | Brexiaceae (Brexioideae) | Penthoraceae (Penthoroideae) |
| Penthoroideae (1) | Eremosynaceae (Eremosynoideae) | Penthoraceae (Penthoroideae) | Grossulariaceae (Ribesoideae, Iteoideae, Pterostemonoideae, Brexioideae, Phyllonomoideae, Escallonioideae, Montinioideae) | Grossulariaceae (Ribesoideae) | Grossulariaceae (Ribesoideae) |
| Tetracarpaeoideae (1) | Vahliaceae (Vahlioideae) | Francoaceae (Francooideae) | Cunoniaceae (Baueroideae) | Iteaceae (Iteoideae) | Iteaceae (Iteoideae) |
| Ribesoideae (1) | Francoaceae (Francooideae) | Grossulariaceae (Ribesoideae) | | Droserales | Francoaceae (Francooideae) |
| Iteoideae (1) | Parnassiaceae (Parnassioideae) | Vahliaceae (Vahlioideae) | | Parnassiaceae (Parnassioideae) | Parnassiaceae (Parnassioideae) |
| Pterostemonoideae (1) | Lignosae | Eremosynaceae (Eremosynoideae) | | Lepuropetalaceae (Lepuropetaloideae) | Lepuropetalaceae (Lepuropetaloideae) |
| Baueroideae (1) | Cunoniales | Lepuropetalaceae (Lepuropetaloideae) | | Corniflorae | Vahliaceae (Vahlioideae) |
| Francooideae (2) | Pterostemonaceae (Pterostemonoideae) | Parnassiaceae (Parnassioideae) | | Cornales | Eremosynaceae (Eremosynoideae) |
| Brexioideae (3) | Philadelphaceae (Hydrangeoidea) | Cunoniales | | Escalloniaceae (Escallonioideae) | Rosidae–Cornanae |
| Parnassioideae (1) | Hydrangeaceae (Hydrangeoideae) | Cunoniaceae (Baueroideae) | | Montiniaceae (Montinioideae) | Hydrangeales |
| Lepuropetaloideae (1) | Grossulariaceae (Ribesoideae) | Cornanae | | Hydrangeaceae (Hydrangeoideae) | Tetracarpaeaceae (Tetracarpaeoideae) |
| Hydrangeoideae (17) | Escalloniaceae (Iteoideae, Escallonioideae, Brexioideae, Phyllonomoideae, Montinioideae, Tetracarpaeoideae) | Hydrangeales | | Dulongiaceae (Phyllonomoideae) | Escalloniaceae (Escallonioideae) |
| Phyllonomoideae (1) | Baueraceae (Baueroideae) | Hydrangeaceae (Hydrangeoideae) | | Eremosynaceae (Eremosynoideae) | Montiniaceae (Montinioideae) |
| Escallonioideae (14) | | Escalloniaceae (Escallonioideae, Iteoideae, Phyllonomoideae, Pterostemonoideae) | | Pterostemonaceae (Pterostemonoideae) | Dulongiaceae (Phyllonomoideae) |
| Montinioideae (2) | | Montiniaceae (Montinioideae) | | Tetracarpaeaceae (Tetracarpaeoideae) | Hydrangeaceae (Hydrangeoideae) |
| Vahlioideae (1) | | Brexiaceae (Brexioideae) | | Cunoniales | Pterostemonaceae (Pterostemonoideae) |
| Eremosynoideae (1) | | | | Baueraceae (Baueroideae) | Rosidae–Celastranae |
| | | | | | Celastrales |
| | | | | | Brexiaceae (Brexioideae) |

fined, consisting of 17 subfamilies: Saxifragoideae, Penthoroideae, Tetracarpaeoideae, Ribesoideae, Iteoideae, Pterostemonoideae, Baueroideae, Francooideae, Brexioideae, Parnassioideae, Lepuropetaloideae, Hydrangeoideae, Phyllonomoideae, Escallonioideae, Montinioideae, Vahlioideae, and Eremosynoideae (Table 1). In this paper, we will use this classification as a reference and will refer to it as Saxifragaceae sensu lato (Saxifragaceae *s. l.*). Saxifragaceae *s. l.* are a heterogeneous assemblage, including annual, biennial, and perennial herbs, shrubs, trees, and woody vines, and also having considerable chemical, anatomical, palynological, and cytological diversity.

Most recent authors have defined Saxifragaceae more narrowly and treated many members of Saxifragaceae *s. l.* either as separate families or as components of other families. Hutchinson (1973; Table 1) separated the woody and herbaceous constituents of Saxifragaceae *s. l.*, allying the woody taxa with Cunoniaceae. Other authors do not draw as sharp a distinction as did Hutchinson but do tend to separate woody from herbaceous taxa. Some classifications (e.g., Cronquist, 1981; Table 1), while defining Saxifragaceae narrowly, nevertheless included most members of Saxifragaceae *s. l.* in one order (Rosales), suggesting a fairly close relationship among them. Others, in contrast (Dahlgren, 1983; Takhtajan, 1987; Thorne, 1992; Table 1), considered some of the herbaceous and woody members of Saxifragaceae *s. l.* to be only distantly related and allied many of the woody taxa with groups such as Cornales.

The widely divergent views regarding the composition and affinities of Saxifragaceae clearly indicate that the family remains enigmatic. Although some experimental research has provided useful insights (e.g., Bensel & Palser, 1975a, b, c, d; Grund & Jensen, 1981; Hideux & Ferguson, 1976), the actual phylogenetic affinities of the taxa composing Saxifragaceae *s. l.* remain poorly understood. Results from a preliminary study of Saxifragaceae *s. l.* using sequence data from the chloroplast gene *rbc*L (Soltis et al., 1990) suggested strongly that this approach should prove useful in unravelling the taxonomic problems surrounding Saxifragaceae *s. l.* This study revealed that several of the constituent subfamilies are only distantly related to one another. We therefore initiated a broad phylogenetic analysis of *rbc*L sequence data from taxa representing not only Saxifragaceae *s. l.*, but also many putative relatives. We also included sequences representing a diverse array of dicot families, with two major objectives. The first objective was to ascertain how best to define Saxifragaceae. Secondly, we hoped to determine potential close relatives of the members of Saxifragaceae *s. l.* based on *rbc*L sequences currently available.

## Materials and Methods

We generated *rbc*L sequences from at least one representative of 16 of the 17 subfamilies of Saxifragaceae *s. l.* (Table 1). The only subfamily not analyzed was Eremosynoideae. Material of this subfamily could not be obtained (despite repeated attempts) because of its restricted distribution in western Australia. Fourteen of the subfamilies consist of only one or two genera (Table 1); hence, the one *rbc*L sequence obtained from each represents a nearly complete generic sampling. The largest subfamilies are Saxifragoideae and Hydrangeoideae, which consist of approximately 30 and 17 genera, respectively. We sequenced at least five representatives from each of these two subfamilies.

The many proposed classifications of Saxifragaceae have resulted in a long list of possible allies of Saxifragaceae *s. l.* We therefore generated one or more *rbc*L sequences from each of several families that have been considered closely related to members of Saxifragaceae *s. l.* in most taxonomic schemes (Crassulaceae, Cephalotaceae, Droseraceae, Greyiaceae, Cunoniaceae and its allies, Gunneraceae, and Rosaceae). Sequences were also generated for many other potentially related families (Pittosporaceae, Roridulaceae, Garryaceae, and Cornaceae and its relatives). Additional *rbc*L sequences representing a diverse array of dicots were also used in our phylogenetic analyses. These sequences were obtained from many other investigators (listed in the Appendix at the end of this issue). Plant material for sequencing was obtained from field collections, plants grown from seed, silica gel-dried leaf material, or, in a few cases, herbarium specimens (information on sources of plant material is also given in the Appendix at the end of this issue). Total DNA was extracted using a CTAB buffer method (Doyle & Doyle, 1987) as modified by Soltis et al. (1991).

### Amplification and Sequencing

With the exception of the eight sequences originally reported from Saxifragaceae *s. l.* (Soltis et al., 1990), *rbc*L was amplified using thermostable DNA polymerase. We performed amplifications using either *Taq* I polymerase (Promega) or Replitherm (Epicentre Technologies) following the directions of the manufacturers. Synthetic oligonucleotides were used as primers. The forward

primer (Z1) represents bases 1–30 of *rbc*L from *Zea mays* L. The reverse primer typically employed (3′ *rbc*L) is external to the 3′ end of the *rbc*L gene. This primer is 34 nucleotides long, corresponds to the sequence of *Nicotiana*, and begins 103 base pairs outside the coding sequence termination of the gene in *Nicotiana* (Olmstead et al., 1992). In several instances we were unable to amplify *rbc*L using this Z1-3′ *rbc*L primer combination. In these taxa, *rbc*L was successfully amplified using an internal reverse primer (Z1351R) in place of the 3′ *rbc*L primer. The Z1351R primer represents bases 1351–1380 of *rbc*L from *Zea mays*.

Two amplifications were performed. A double stranded reaction with both forward and reverse primers was first performed. The double stranded product was subsequently used as a template in an amplification using only one primer to produce single-stranded DNA for sequencing. Single-stranded DNA was then purified by precipitation with a 20% PEG/2.5 M NaCl solution, washes in 70% and 95% ethanol, and resuspension in 1 × TE.

Purified single-stranded products were sequenced directly. Both forward and reverse strands were sequenced using 30-mer primers corresponding to the *rbc*L sequence of *Zea mays*. These primers were kindly provided by G. Zurawski; six sequencing primers were used for each strand. Dideoxy sequencing reactions were performed using the Sequenase version 3.1 kit (United States Biochemicals) and $^{35}$S dATP. Fragments were separated at 2,000 volts/70 watts in 6% polyacrylamide gels (0.4 mm thick), using 1 × TBE buffer. Gels were fixed with 10% acetic acid, washed with distilled water, dried, and used to expose Kodak X-Omat AR film for 16–24 hours.

A total of 1,377 base pairs of *rbc*L (bases 31–1407) was standardly used for analysis. Several of our sequences from Saxifragaceae *s. l.* were amplified by cloning (Soltis et al., 1990). Because the cloning site was just inside the 3′ end of the gene, our sequence data for these taxa do not extend past base pair 1407. Therefore, our comparisons herein involve *rbc*L sequence data up to base pair 1407. The first 30 base pairs were also not used because, after amplification, this portion of the gene is identical to the Z1 forward amplification primer. Most taxa were amplified with the external reverse primer (3′ *rbc*L), but *Chrysobalanus*, *Licania*, *Kalanchoe*, *Crassula*, *Sedum*, *Dudleya*, and *Eucryphia* could only be amplified with the internal reverse primer (Z1351R), and for these seven taxa 1,320 base pairs of sequence data (bases 31–1350) were used.

PHYLOGENETIC ANALYSIS

Sequence data were analyzed using PAUP version 3.0s (Swofford, 1991). Because the various *rbc*L-supported lineages of Saxifragaceae *s. l.* are allied with so many distantly related taxa, several phylogenetic analyses were necessary to best determine potential relatives of all the component subfamilies. These analyses were carried out using the results of a previous broad analysis as an initial framework (Chase et al., 1993).

According to Maddison (1991), multiple "islands," or separate clusters, of most parsimonious trees are likely to be present for a given data set, especially if it includes a large number of taxa. To maximize our chances of finding as many shortest trees as possible, we performed as part of each analysis a series of searches aimed specifically at finding multiple islands of trees.

Two primary tree search methods were employed. In the first method, 200 consecutive searches were performed without MULPARS using random taxon addition and nearest-neighbor-interchange (NNI) branch-swapping. This search normally resulted in one to three relatively short trees. Each of the shortest trees resulting from this search was used as the starting tree for a subsequent search with MULPARS using tree-bisection-reconnection (TBR) branch-swapping. This set of analyses was repeated several times (each time a different random number seed for the NNI search was used) with the TBR tree searches each beginning with a different starting tree, the expectation being that several analyses with different starting trees would find multiple islands of shortest trees if they exist.

In the second tree search method employed, 50 consecutive searches were performed with MULPARS using random taxon addition and TBR branch-swapping. To reduce the amount of time involved, the program was allowed to save no more than ten trees of any length longer than that of the shortest trees found by using the first method, above. This second search strategy was recommended by Swofford (1991). We compared the results of these two search methods with those obtained using a widely employed method of analysis: a single search using simple taxon addition and TBR branch-swapping. The results of these comparisons will be discussed below.

Our initial broad analysis included all of our representatives of Saxifragaceae *s. l.* and putative relatives plus a broad sampling of non-magnoliid dicots. This analysis included 100 taxa and was performed to: (1) obtain a rough approximation of

likely alliances of the members of Saxifragaceae *s. l.* and (2) help focus subsequent, more detailed analyses of smaller groups that include members of Saxifragaceae *s. l.* The initial broad analysis made use of the first search method described above and involved three separate tree searches, each with a different starting tree. The resulting trees were rooted with an outgroup consisting of *Tetracentron*, *Trochodendron*, *Sabia*, and *Platanus* because in the broad analysis of Chase et al. (1993) these genera were identified as sister taxa to the group that we analyzed.

With the results of our initial broad analysis as a guide, four subsequent, more detailed analyses were conducted using subsets of the larger data set to identify more accurately potential relatives of taxa of Saxifragaceae *s. l.* For each of these four subsequent analyses portions of the *rbc*L-based phylogeny resulting from our initial broad analysis were selected, with particular attention given to groups that occurred in the results of both our initial analysis and that of Chase et al. (1993). Additional sequences were added to the four groups based on the results of the analysis of Chase et al. (1993) so that each group would contain greater taxon density. For each of these four analyses, an outgroup was specified consisting of five taxa that were closely related to and basal to the group being analyzed. Tree searches for these four analyses employed both primary search methods described above. Seven separate TBR searches were conducted using the first method. Because some of these analyses resulted in very few shortest trees, we decided to perform further analyses using the second search method, hoping to find additional shortest trees. Three of the four groups were also subjected to bootstrap analyses, which were performed using 100 replicates, simple taxon addition, TBR branch-swapping, and MULPARS.

## Results

We have chosen to show for our initial broad analysis, as well as our four subsequent smaller analyses, the 50% majority-rule consensus tree because it effectively summarizes the major features present among all shortest trees. Additionally, we have constructed each majority-rule consensus tree so that it includes compatible groupings of less than 50% occurrence. For our broad analysis and our four smaller analyses we obtained in each case a consensus tree identical to one of the shortest trees; thus we can place nucleotide substitutions on these trees (Figs. 1–5).

Our initial broad analysis of 100 sequences included three separate tree searches, each of which found a different island of trees. The first search found 351 trees, 3,811 steps long, the second found 27 trees, 3,811 steps long, and the third found nonminimal trees (3,812 steps long). The majority-rule consensus tree was constructed from the 378 trees that were 3,811 steps long (Fig. 1). Two portions of this tree were selected for further analysis (see Fig. 1). For convenience we will refer to them as the "rosid clade" and the "asterid clade," although both include many taxa normally included in other subclasses.

Analysis of the rosid clade resulted in 16 shortest trees, 3,060 steps long, in two islands of eight trees each (Fig. 2). The second search method found both islands, but one of the two islands was not found by the first search method or by the single analysis using simple taxon addition. One of the objectives of our analysis was to obtain information on the amount of support for alliances involving members of Saxifragaceae *s. l.* using bootstrap analysis. Because of the size of the rosid clade (86 taxa) it was necessary to conduct further analyses of the group by dividing it into two smaller parts, which we will refer to as rosid groups A and B. Group B consists of an alliance of 61 taxa taken from within the rosid clade, a group supported by 10 nucleotide substitutions (see Fig. 2). A second group (group A) was formed to accomplish further analysis of the remaining taxa of the rosid clade (i.e., those outside of group B). For this analysis, the number of taxa in the rosid clade was reduced by deleting 31 sequences from among those included in group B. Group A, therefore, included the same taxa as did the rosid clade, except that group B was represented in the analysis by 30 taxa rather than 61 (see Fig. 2).

Analysis of rosid group A resulted in 12 shortest trees, 2,000 steps long, in only one island (Fig. 3). These 12 trees were found by both primary search methods and by the single analysis using simple taxon addition. The taxa that we will emphasize as part of group A include representatives of "core" Saxifragaceae (i.e., subfamily Saxifragoideae) as well as genera representing five other subfamilies: *Itea* (Iteoideae), *Pterostemon* (Pterostemonoideae), *Ribes* (Ribesoideae), *Penthorum* (Penthoroideae), and *Tetracarpaea* (Tetracarpaeoideae).

Analysis of rosid group B resulted in 40 shortest trees, 2,584 steps long, in four islands of 2, 4, 14, and 20 trees (Fig. 4). All four islands of shortest trees were found by both primary search methods, but the single analysis using simple taxon addition found only the island consisting of two trees. Representatives of several subfamilies of Saxifragaceae

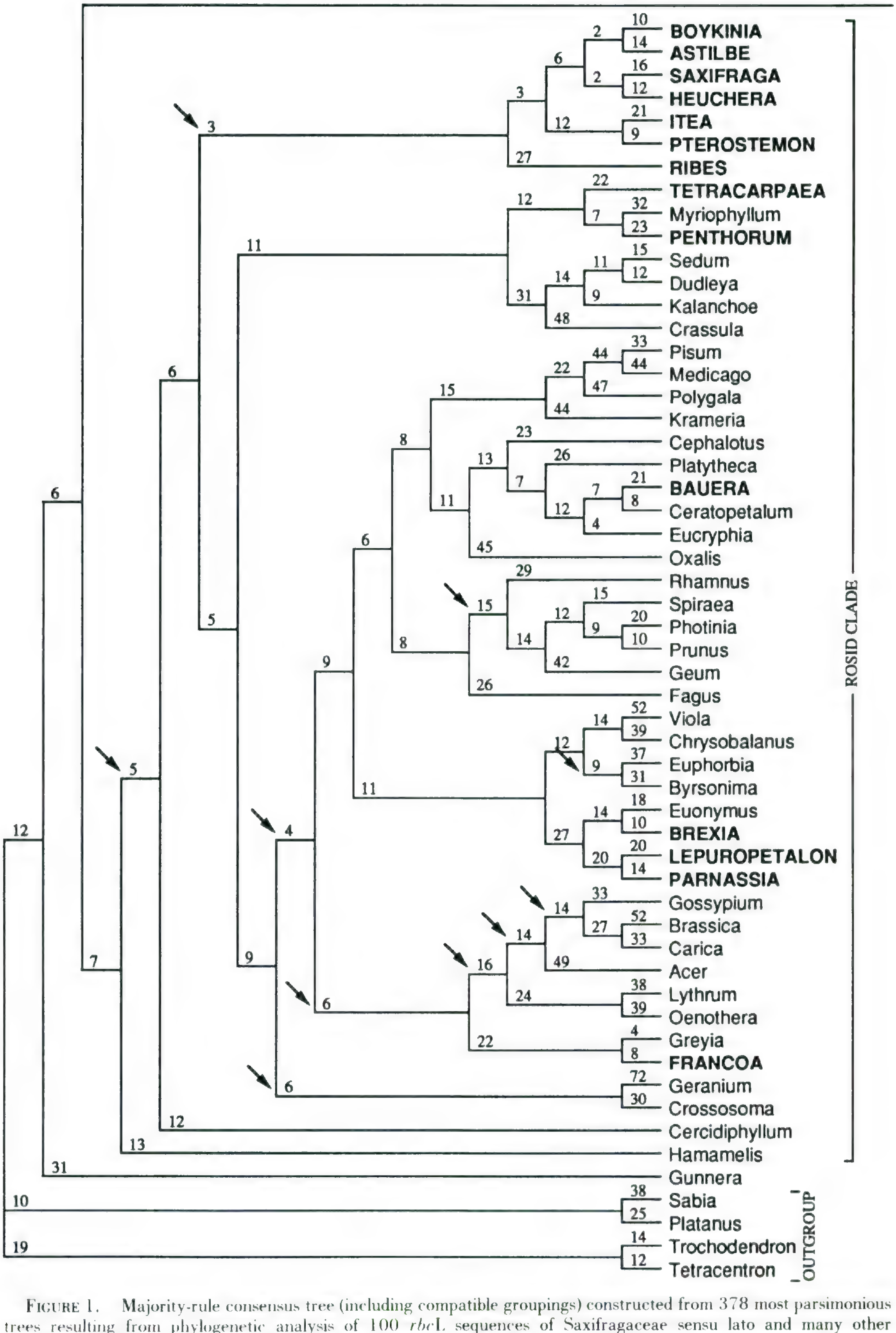
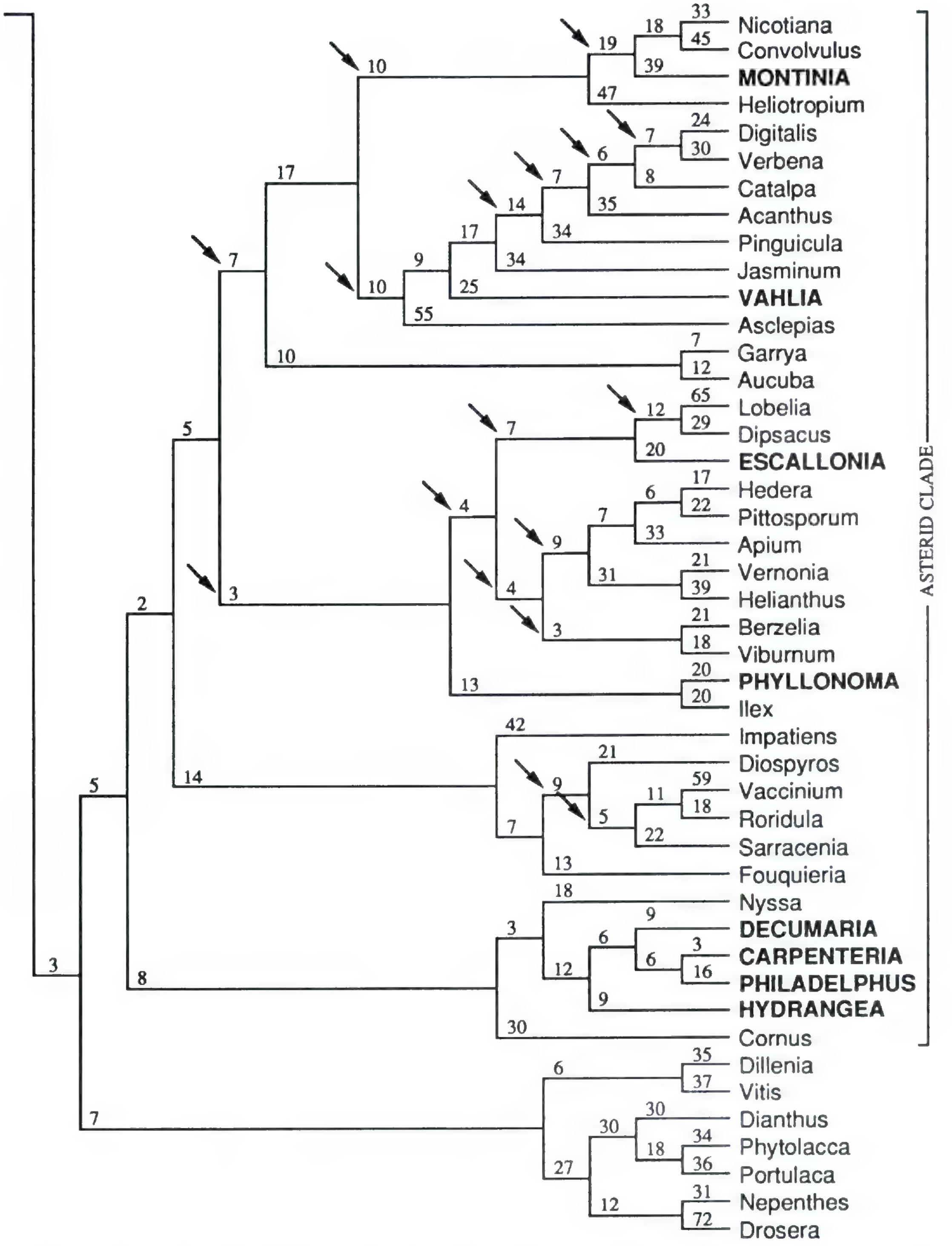
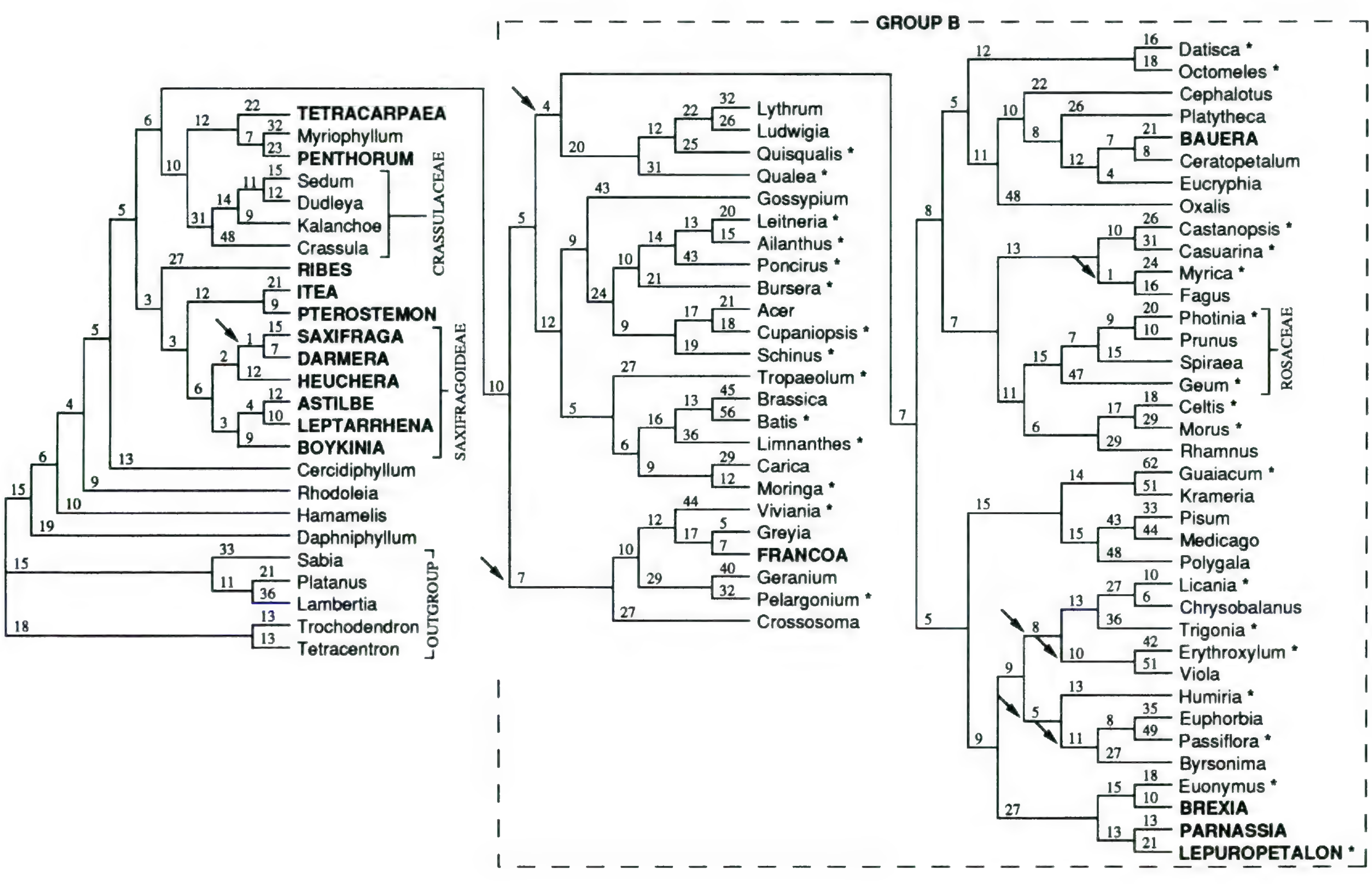



FIGURE 1. Majority-rule consensus tree (including compatible groupings) constructed from 378 most parsimonious trees resulting from phylogenetic analysis of 100 *rbc*L sequences of Saxifragaceae sensu lato and many other nonmagnoliid dicots. This tree is identical to one of the 378 shortest trees and has a consistency index of 0.266 and




a retention index of 0.46. Arrows point to nodes that did not occur in all shortest trees; all other nodes were present in all 378 most parsimonious trees. Numbers above each branch indicate the number of base substitutions. Names of taxa of Saxifragaceae sensu lato are shown in capital letters and boldface type. The two portions of the tree selected for further analysis (the rosid clade and the asterid clade) are indicated by brackets and labeled.


GROUP B
TETRACARPAEA
Myriophyllum
PENTHORUM
Sedum
Dudleya
Kalanchoe
Crassula
CRASSULACEAE
RIBES
ITEA
PTEROSTEMON
SAXIFRAGA
DARMERA
HEUCHERA
ASTILBE
LEPTARRHENA
BOYKINIA
SAXIFRAGOIDEAE
Cercidiphyllum
Rhodoleia
Hamamelis
Daphniphyllum
Sabia
Platanus
Lambertia
Trochodendron
Tetracentron
OUTGROUP
Lythrum
Ludwigia
Quisqualis *
Qualea *
Gossypium
Leitneria *
Ailanthus *
Poncirus *
Bursera *
Acer
Cupaniopsis *
Schinus *
Tropaeolum *
Brassica
Batis *
Limnanthes *
Carica
Moringa *
Viviania *
Greyia
FRANCOA
Geranium
Pelargonium *
Crossosoma
Datisca *
Octomeles *
Cephalotus
Platytheca
BAUERA
Ceratopetalum
Eucryphia
Oxalis
Castanopsis *
Casuarina *
Myrica *
Fagus
Photinia *
Prunus
Spiraea
Geum *
ROSACEAE
Celtis *
Morus *
Rhamnus
Guaiacum *
Krameria
Pisum
Medicago
Polygala
Licania *
Chrysobalanus
Trigonia *
Erythroxylum *
Viola
Humiria *
Euphorbia
Passiflora *
Byrsonima
Euonymus *
BREXIA
PARNASSIA
LEPUROPETALON *

*s. l.* are included in group B: *Francoa* (Francooideae), *Bauera* (Baueroideae), *Brexia* (Brexioideae), *Parnassia* (Parnassioideae), and *Lepuropetalon* (Lepuropetaloideae).

Analysis of the asterid clade resulted in 36 shortest trees, 1,496 steps long, in one island (Fig. 5). These 36 trees were found by both primary search methods and by the single analysis using simple taxon addition. The asterid clade includes, in addition to many taxa usually included in subclass Asteridae (sensu Cronquist, 1981), representatives of five subfamilies of Saxifragaceae *s. l.*: *Escallonia* (Escallonioideae), *Phyllonoma* (Phyllonomoideae), *Vahlia* (Vahlioideae), *Montinia* (Montinioideae), and five genera of Hydrangeoideae. According to our *rbc*L sequence data, all of these taxa are distantly related to core members of Saxifragaceae (Olmstead et al., 1993, have conducted more detailed analyses of taxa in Asteridae).

## Discussion

Our phylogenetic analysis of *rbc*L sequences indicates that the taxa traditionally included in Saxifragaceae *s. l.* are not a monophyletic assemblage. Rather, they are allied with at least ten different, often very distantly related, lineages representing most of the traditionally recognized subclasses of dicots (Fig. 1). The results of this analysis do not correspond closely with any proposed classification of Saxifragaceae; in many cases *rbc*L sequence data suggest relationships that differ substantially from traditional classifications. For ease of presentation, we will discuss the systematic implications of this study by examining the relationships of each of the subfamilies of Saxifragaceae *s. l.* individually. Our discussion will be divided into five parts corresponding to more inclusive alliances involving the subfamilies of Saxifragaceae *s. l.*: I. Saxifragoideae and associated subfamilies (Saxifragoideae, Iteoideae, Pterostemonoideae, Ribesoideae); II. Subfamilies associated with Crassulaceae (Penthoroideae, Tetracarpaeoideae); III. Subfamilies associated with other families of Rosidae (Baueroideae, Francooideae, Brexioideae, Parnassioideae, Lepuropetaloideae); IV. Subfamilies associated with Cornaceae (Hydrangeoideae); V. Subfamilies associated with Asteridae (Phyllonomoideae, Escallonioideae, Montinioideae, Vahlioideae).

### I. Saxifragoideae and associated subfamilies

*Saxifragoideae.* It is generally agreed that approximately 30 genera placed in Saxifragoideae (Table 1) comprise a natural group. These taxa share many morphological, anatomical, and chemical features, and most classifications maintain these genera as a distinct group at the familial, subfamilial, or tribal level. Saxifragoideae are the core of the original Saxifragaceae *s. l.* and some classifications define Saxifragaceae so narrowly that the family consists only of this subfamily or perhaps a few additional taxa. For example, the Saxifragaceae of Takhtajan (1987) and Thorne (1992) are basically equivalent to Schulze-Menz's subfamily Saxifragoideae. Saxifragaceae as defined by Hutchinson (1973) and Dahlgren (1983) consist only of Saxifragoideae and a few genera from other subfamilies of Saxifragaceae *s. l.*. Other classifications (e.g., Cronquist, 1981) include still additional genera in the family.

The results of our analyses support the monophyly of Saxifragoideae by defining a monophyletic group composed of six genera of the subfamily (Figs. 2, 3). These data also suggest that many subfamilies that have been combined with Saxifragoideae to form broader versions of Saxifragaceae (e.g., Parnassioideae, Lepuropetaloideae, Penthoroideae, Francooideae, Vahlioideae; Fig. 1) are distantly related to Saxifragoideae.

The distinctiveness of Saxifragoideae and the distant relationships between them and other subfamilies are confirmed by other molecular data. Downie et al. (1991) have determined that some angiosperms lack the intron of the chloroplast gene *rpl2*. Significantly, this intron is absent in all tested species of Saxifragoideae but present in genera from all other subfamilies of Saxifragaceae *s. l.* examined (Iteoideae, Ribesoideae, Francooideae, Penthoroideae, Brexioideae, Escallonioideae, Par-

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Figure 2. Majority-rule consensus tree (including compatible groupings) constructed from 16 most parsimonious trees resulting from phylogenetic analysis of *rbc*L sequences of the rosid clade. This tree is identical to one of the 16 shortest trees and has a consistency index of 0.293 and a retention index of 0.496. Arrows point to nodes that did not occur in all shortest trees; all other nodes were present in all 16 most parsimonious trees. Numbers above each branch indicate the number of base substitutions. Names of taxa of Saxifragaceae sensu lato are shown in capital letters and boldface type. Rosid group B, selected for further analysis, is indicated by a bracket and labeled. Taxa not included in the rosid group A analysis are indicated by asterisks.

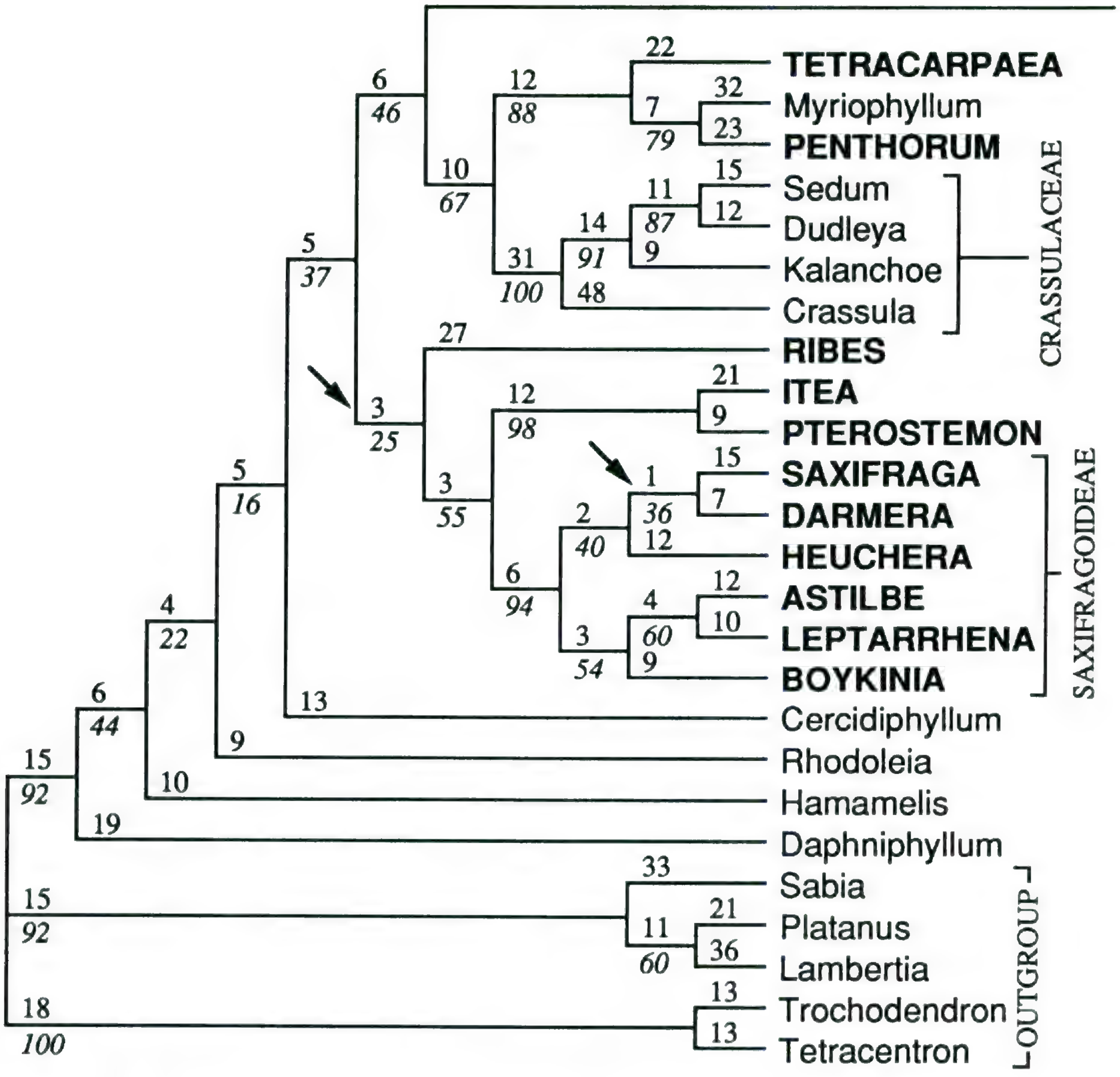


FIGURE 3. Majority-rule consensus tree (including compatible groupings) constructed from 12 most parsimonious trees resulting from phylogenetic analysis of *rbc*L sequences of rosid group A. This tree is identical to one of the 12 shortest trees and has a consistency index of 0.374 and a retention index of 0.473. Arrows point to nodes that did not occur in all shortest trees; all other nodes were present in all 12 most parsimonious trees. Numbers above each branch indicate the number of base substitutions; numbers in italics below each branch indicate the percentage occurrence of each monophyletic group in the results of 100 bootstrap replicates. Names of taxa of Saxifragaceae sensu lato are shown in capital letters and boldface type.

nassioideae, Hydrangeoideae). Downie et al. (1991) suggested that the *rpl*2 intron has been lost in six separate angiosperm lineages, one of them being Saxifragoideae. Chloroplast DNA restriction site data (Soltis et al., 1993) likewise support Saxifragoideae being a distinct group. According to cpDNA restriction site data, Saxifragoideae are a well-supported monophyletic group separate from *Ribes* and *Francoa*, two taxa that have very often been associated with it. These three lines of evidence suggest that the family Saxifragaceae would be best defined as comprising only subfamily Saxifragoideae (sensu Schulze-Menz, 1964) and that other subfamilies of Saxifragaceae *s. l.* should be treated either as separate families or as members of other families. This narrow definition of Saxifragaceae is identical to the concept of the family proposed by Takhtajan (1987) and Thorne (1992).

In addition to helping resolve a long-standing taxonomic problem (the composition of Saxifragaceae), *rbc*L sequence data are of value in identifying potential close relatives of this narrowly defined group and in determining the possible affinities of the other subfamilies of Saxifragaceae *s.*

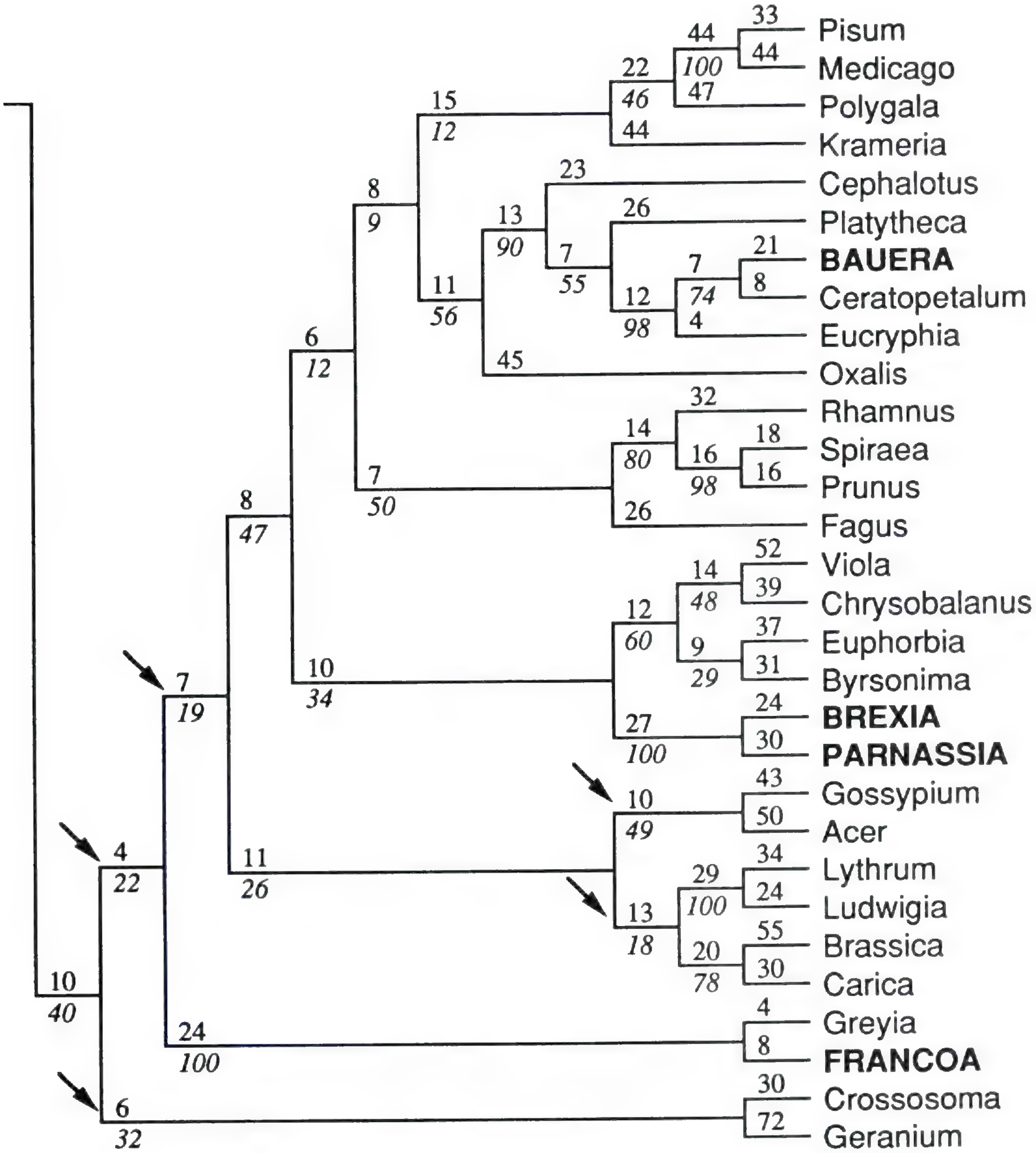


FIGURE 3. Continued.

*l.* In the following sections we will discuss the systematic implications of *rbc*L sequence data for the remaining subfamilies of Saxifragaceae *s. l.*

*Iteoideae.* Our *rbc*L sequence evidence suggests that *Itea*, the only genus in Iteoideae, is closely related to Saxifragoideae (Figs. 2, 3). *Itea* has at times been associated with herbaceous rather than with woody Saxifragaceae *s. l.* (Dahlgren, 1983; Takhtajan, 1987), but has also been placed nearer the woody subfamilies by some (Cronquist, 1981; Hutchinson, 1973; Thorne, 1992). Sequence data, however, suggest that *Itea* is clearly separated from most other woody subfamilies (Figs. 1–3).

Previous investigations have provided conflicting results regarding the alliances of *Itea*. According to Spongberg (1972), chambered pith and stipulate leaves distinguish *Itea* from Escallonioideae. Embryologically, *Itea*, which has bitegmic and crassinucellate ovules, is identical to Saxifragoideae, as well as Ribesoideae, and distinct from Hydrangeoideae, Escallonioideae, and Montinioideae, which have unitegmic tenuinucellate ovules (Table 2).

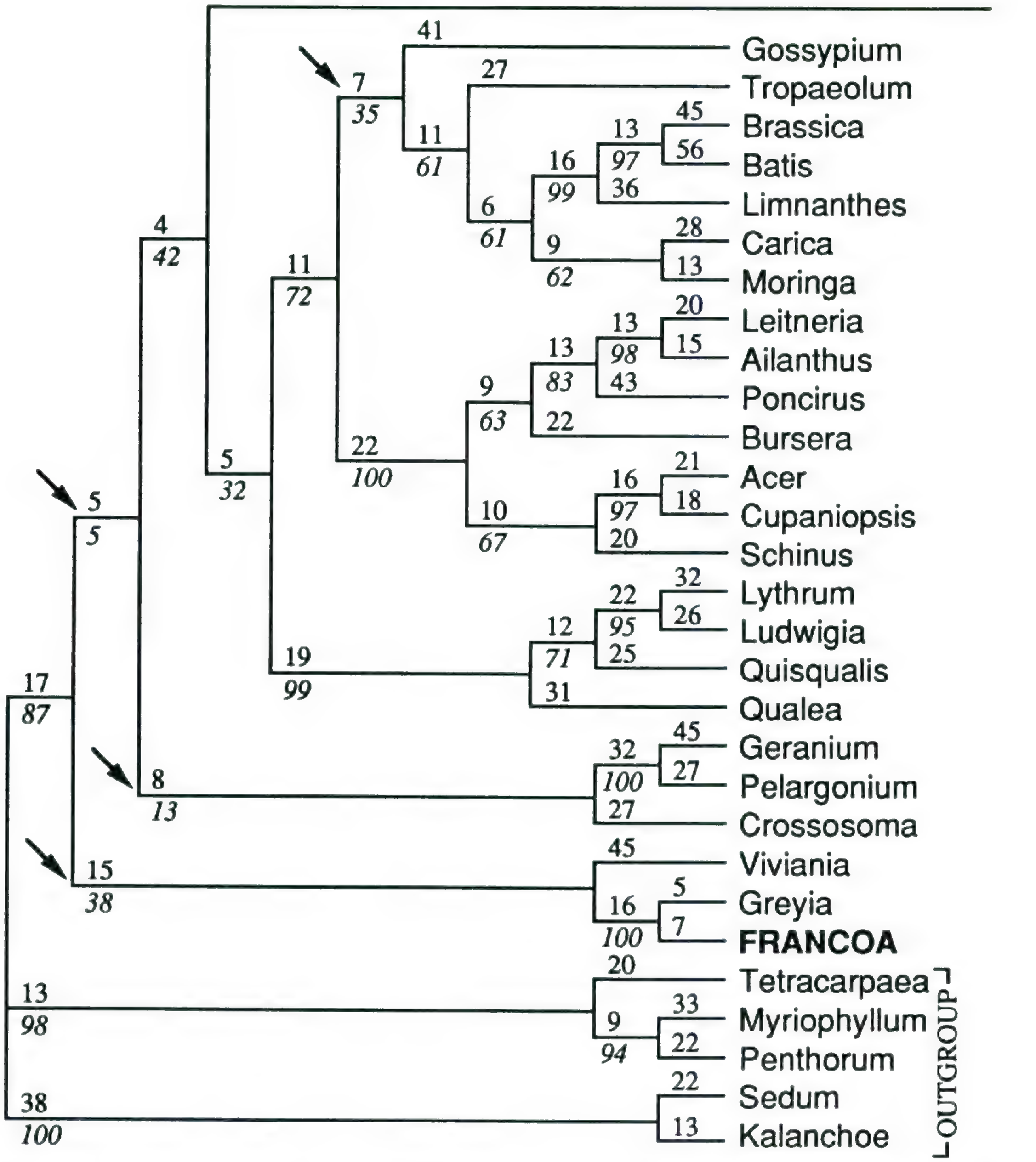


FIGURE 4. Majority-rule consensus tree (including compatible groupings) constructed from 40 most parsimonious trees resulting from phylogenetic analysis of *rbc*L sequences of rosid group B. This tree is identical to one of the 40 shortest trees and has a consistency index of 0.326 and a retention index of 0.476. Arrows point to nodes that did not occur in all shortest trees; all other nodes were present in all 40 most parsimonious trees. Numbers above each branch indicate the number of base substitutions; numbers in italics below each branch indicate the percentage occurrence of each monophyletic group in the results of 100 bootstrap replicates. Names of taxa of Saxifragaceae sensu lato are shown in capital letters and boldface type.

Also, Bensel & Palser (1975b, d) found morphological and anatomical characteristics of the flowers of *Itea* to be virtually identical to those of Saxifragoideae, and noted that it was essentially impossible to differentiate between flowers of *Itea* and Saxifragoideae, externally or internally.

In contrast, other lines of evidence suggest that *Itea* is more closely related to other woody subfamilies. Hamel (1953) concluded, on the basis of karyological data, that *Itea* was most closely allied with *Escallonia*. The pollen of *Itea* is bilateral and two-porate (Hideux & Ferguson, 1976; Spongberg,

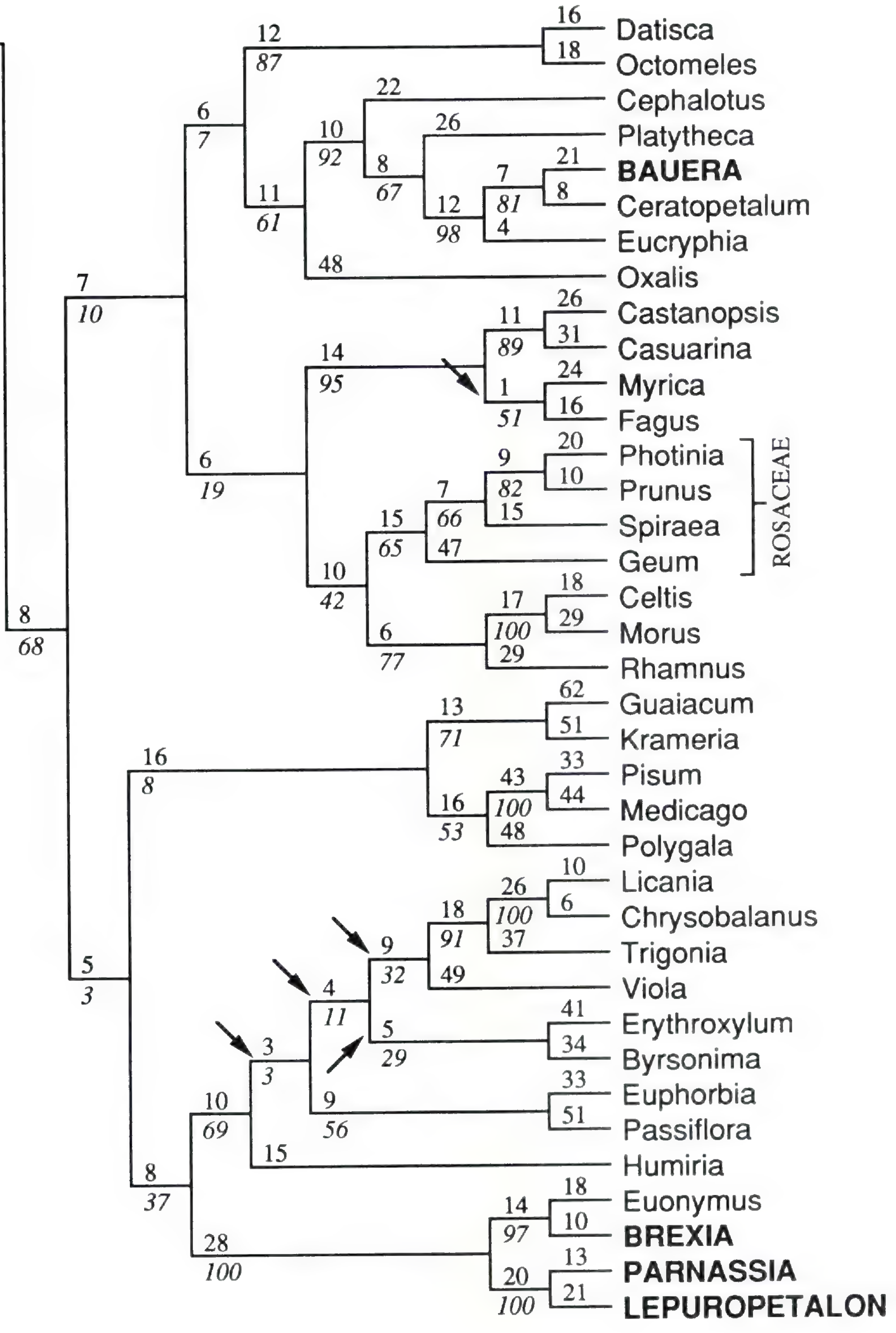


FIGURE 4. Continued.

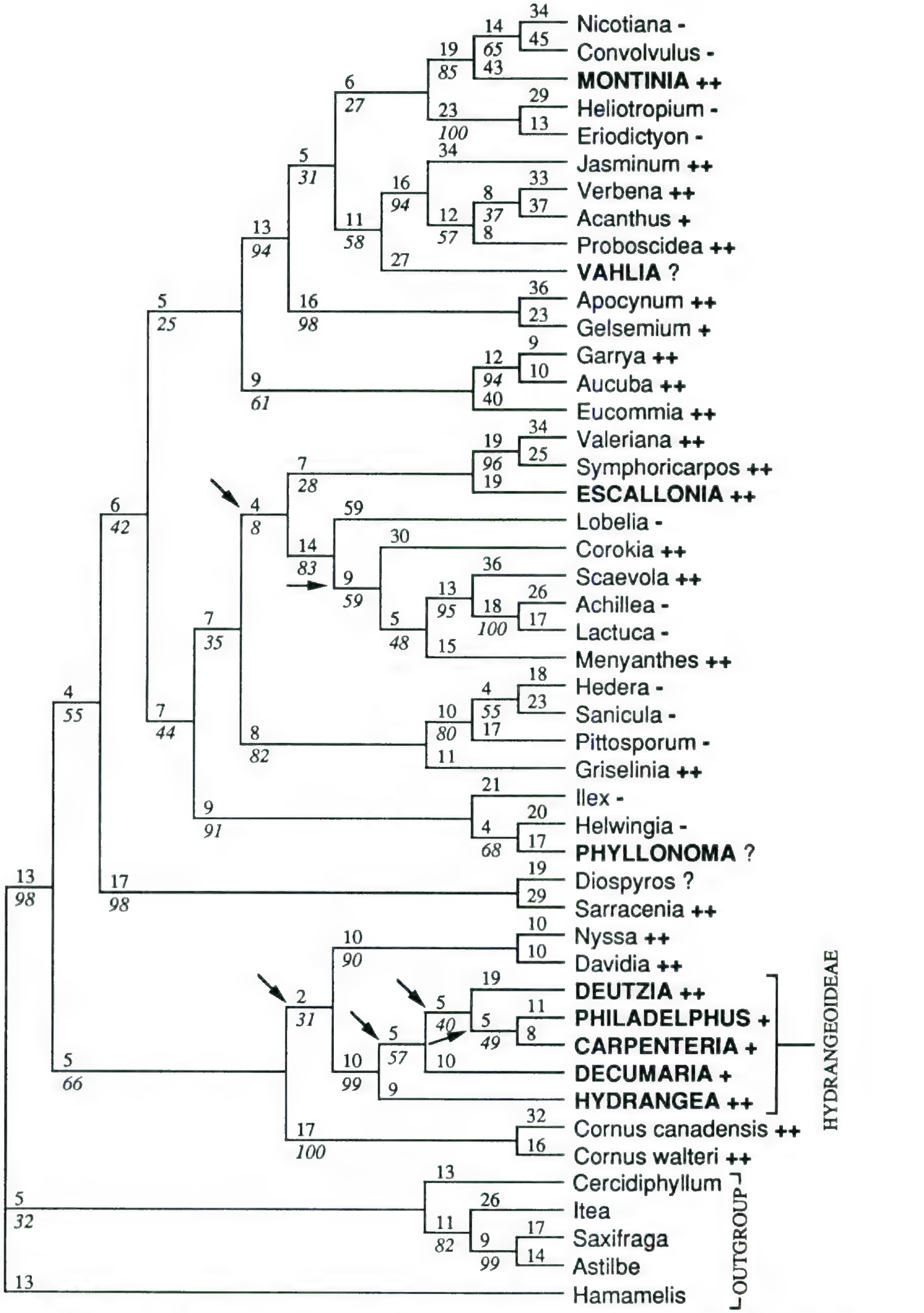


FIGURE 5. Majority-rule consensus tree (including compatible groupings) constructed from 36 most parsimonious trees resulting from phylogenetic analysis of *rbc*L sequences of the asterid clade. This tree is identical to one of the

TABLE 2. Embryological characteristics of the subfamilies of Saxifragaceae sensu lato and additional related families. Sources: Dahlgren (1975b, 1983); Davis (1966); Philipson (1974, 1977); Schulze-Menz (1964); Sharma (1968); Spongberg (1972). Types of endosperm formation: "N" = nuclear; "C" = ab initio cellular; "H" = helobial; "?" = unknown.

| Taxa | Number of integuments | Nucellus | Endosperm type |
|---|---|---|---|
| Saxifragoideae | 2 | crassinucellate | C, H |
| Penthoroideae | 2 | crassinucellate | C |
| Tetracarpaeoideae | 2 | crassinucellate | ? |
| Ribesoideae | 2 | crassinucellate | C, H |
| Iteoideae | 2 | crassinucellate | ? |
| Pterostemonoideae | 2 | crassinucellate | ? |
| Baueroideae | 2 | crassinucellate | N |
| Francooideae | 2 | crassinucellate | N |
| Brexioideae | 2 | tenuinucellate | N |
| Parnassioideae | 2 | tenuinucellate | N |
| Lepuropetaloideae | 1 | ? | ? |
| Hydrangeoideae | 1 | tenuinucellate | C |
| Phyllonomoideae | 1 | ? | ? |
| Escallonioideae | 1 | tenuinucellate | N |
| Montinioideae | 1 | tenuinucellate | ? |
| Vahlioideae | 2 | tenuinucellate | C |
| Eremosynoideae | 1 | tenuinucellate | ? |
| Aquifoliaceae | 1 | crassinucellate, tenuinucellate | C |
| Celastraceae | 2 | crassinucellate, tenuinucellate | N |
| Cornaceae | 1 | crassinucellate, tenuinucellate | C |
| Crassulaceae | 2 | crassinucellate | C |
| Cunoniaceae | 2 | crassinucellate | N |
| Greyiaceae | 2 | crassinucellate | N |
| Haloragaceae | 2 | crassinucellate | C |

1972). This is an extremely uncommon pollen type, apparently found elsewhere only in *Choristylis*, which is usually included in Escallonioideae. In other pollen characteristics, *Itea* is very much like several genera in Escallonioideae, and the complete tectum and reduced ectoaperture of its pollen further distinguish *Itea* from Saxifragoideae.

Chemical evidence generally suggests that *Itea* is distinct from Saxifragoideae and more closely allied with other woody taxa. Plouvier (1965) found allitol in *Itea* and dulcitol in *Brexia*. He proposed a close alliance between the two because allitol and dulcitol are isomers, and allitol was not found in genera of Saxifragoideae. Plouvier furthermore suggested that both *Itea* and *Brexia* were related to Celastraceae, members of which also accumulate dulcitol. Jay (1970) reported that *Itea* and *Brexia* were essentially identical in flavonoid characteristics, having equal amounts of leucodelphinidine and leucocyanidine and lacking flavonols. Jay advocated a close relationship between *Itea* and *Brexia* and an alliance between them and *Escallonia*. Bohm et al. (1988) confirmed the absence of flavonols in *Itea* and remarked that, while many members of Saxifragaceae *s. l.* (both herbaceous and woody taxa from several subfamilies) produce flavonols,

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36 shortest trees and has a consistency index of 0.428 and a retention index of 0.486. Arrows point to nodes that did not occur in all shortest trees; all other nodes were present in all 36 most parsimonious trees. Numbers above each branch indicate the number of base substitutions; numbers in italics below each branch indicate the percentage occurrence of each monophyletic group in the results of 100 bootstrap replicates. Names of taxa of Saxifragaceae sensu lato are shown in capital letters and boldface type. Occurrence of iridoids is indicated for all taxa: "++" = genera known to produce iridoids, "+" = genera that have not been studied but are members of families known to have iridoids, "−" = genera and members of families that are known not to produce iridoids, "?" = unknown for iridoid occurrence. Sources of data on iridoid occurrence: Dahlgren et al. (1977, 1981); Jensen et al. (1975); Kaplan & Gottlieb (1982).

*Itea* is virtually alone in that it accumulates only flavones.

Our data provide no support for a close alliance between *Itea* and Cornales (Dahlgren, 1983; Takhtajan, 1987) or for the contentions of Plouvier (1965) and Jay (1970) that *Itea* is closely related to *Brexia*. According to *rbc*L sequence data, *Itea* is only distantly related to woody subfamilies such as Hydrangeoideae, Escallonioideae, and Montinioideae. Sequence results of *rbc*L suggesting a close relationship between *Itea* and Saxifragoideae are intriguing and parallel embryological characters and the floral data of Bensel & Palser (1975b, d). The closest relative of *Itea* may be the subfamily discussed below, Pterostemonoideae.

*Pterostemonoideae.* Evidence from *rbc*L sequences suggests that there is a close alliance between *Pterostemon* and *Itea* (Figs. 2, 3). The monogeneric subfamily Pterostemonoideae consists of shrubs native to Mexico and has traditionally been classified with the woody subfamilies Hydrangeoideae, Escallonioideae, and Montinioideae. However, the position of *Pterostemon* is usually described as uncertain (Cronquist, 1981; Dahlgren, 1983; Hutchinson, 1973; Takhtajan, 1987). As with the woody genus *Itea*, *Pterostemon* is more closely allied in our results with Saxifragoideae than with Hydrangeoideae, Escallonioideae, and Montinioideae.

Embryological characteristics corroborate the placement of *Pterostemon* suggested by *rbc*L sequence data. As with Saxifragoideae and *Itea*, *Pterostemon* is crassinucellate and bitegmic (Table 2), thus the genus is distinct from the tenuinucellate and unitegmic Hydrangeoideae, Escallonioideae, and Montinioideae. Saxifragoideae and *Itea* also have cellular endosperm formation. The type of endosperm present in *Pterostemon* is, however, not known. The presence of cellular endosperm formation in *Pterostemon* might add to the support for its alliance with Saxifragoideae and *Itea*.

In contrast to embryological characters, some morphological and palynological features do not seem to support a close alliance among *Pterostemon*, Saxifragoideae, and *Itea*. *Pterostemon* has, in addition to five fertile stamens, five staminodes. It also has five carpels and little endosperm. *Itea* and Saxifragoideae usually have two carpels, copious endosperm, and no staminodes.

Hideux & Ferguson (1976) described the pollen of *Pterostemon* as having a complete tectum, long ectoaperture, and a complex endoaperture, characteristics most similar to certain escallonioid genera. The tectum surface of *Pterostemon* is much like that of *Itea*, although the short ectoaperture of *Itea* differs from the condition in *Pterostemon*. Hideux & Ferguson (1976) did not, however, include *Pterostemon* in their numerical analysis that included many more pollen characters. They also provided no further description of its pollen, and they had little to say about its possible relationships. According to the description of Erdtman (1966), the pollen of *Pterostemon* may not be similar to that of *Itea*, but with the incomplete descriptions of *Pterostemon* pollen given by both Erdtman (1966) and Hideux & Ferguson (1976), a more detailed palynological study is warranted.

*Pterostemon* has not been studied in great detail; little is known about its wood anatomy, floral anatomy, detailed embryological features, or secondary chemistry. Chemical, anatomical, and additional molecular evidence for *Pterostemon* might help resolve the relationships of this poorly understood genus. For example, given the unique flavonoid profile of *Itea*, secondary chemical data for *Pterostemon* should prove useful.

*Ribesoideae.* The results of *rbc*L sequence analysis indicate that the monogeneric, woody subfamily Ribesoideae is more closely related to Saxifragoideae than to such woody groups as Hydrangeoideae, Escallonioideae, and Montinioideae (Figs. 1–3). Like *Itea*, *Ribes* has been placed close to Saxifragoideae and other herbaceous members of Saxifragaceae *s. l.* (Dahlgren, 1983; Engler, 1928; Takhtajan, 1987; Thorne, 1992), although some (Cronquist, 1981; Hutchinson, 1973) place it closer to other woody members of Saxifragaceae *s. l.*

Many studies have pointed to a close relationship between *Ribes* and Saxifragoideae, and a distant relationship between *Ribes* and other woody taxa. Hamel (1953) found *Ribes* to be homogeneous cytologically ($n = 8$) and advocated placing it very near to, but distinct from Saxifragoideae. Xylem anatomy and embryological characters (Huber, 1963) also support a close relationship between *Ribes* and Saxifragoideae. Gelius (1967) found the floral morphology of *Ribes* to resemble that of Saxifragoideae much more closely than that of other woody Saxifragaceae *s. l.* Similarly, Bensel & Palser (1975a, d) found numerous features of floral anatomy shared by *Ribes* and Saxifragoideae and concluded that, according to floral features alone, *Ribes* should be included in Saxifragoideae.

Plouvier (1965) found that the absence of certain secondary chemicals in *Ribes* distinguished the genus from Saxifragoideae, but he also noted that there were chemical similarities suggesting a close alliance. Jay (1970) stated that flavonoid data

also support a close relationship between *Ribes* and Saxifragoideae. Serological data (Grund & Jensen, 1981) likewise indicate a close relationship between *Ribes* and Saxifragoideae and a distant relationship between *Ribes* and other woody Saxifragaceae *s. l.* The combination of bitegmic crassinucellate ovules with cellular or helobial endosperm formation (Dahlgren, 1975b; Philipson, 1974, 1977; Table 2) also supports a close relationship between *Ribes* and Saxifragoideae.

The pollen of *Ribes*, however, is distinct from most Saxifragoideae. *Ribes* is distinguished from Saxifragoideae in having pollen that is 8–9-aperturate and spheroidal (Erdtman, 1966) with a complete, smooth tectum (Hideux & Ferguson, 1976). The pollen of *Ribes* is most similar to that of certain genera of Escallonioideae and, according to Hideux & Ferguson (1976), it could be accommodated in a broadly defined Escallonioideae including many other woody genera.

Results of *rbc*L sequence analysis agree with most experimental data in placing *Ribes* distant from such woody groups as Hydrangeoideae, Escallonioideae, and Montinioideae. Our data also suggest a relationship between Ribesoideae and the Saxifragoideae–Iteoideae–Pterostemonoideae group, although support for the alliance is low (Figs. 2, 3).

### II. SUBFAMILIES ASSOCIATED WITH CRASSULACEAE

*Penthoroideae.* Our *rbc*L sequence data suggest that *Penthorum* (the only genus of Penthoroideae) is part of an alliance including Crassulaceae and is most closely related to *Myriophyllum* (Haloragaceae; Figs. 2, 3). There has been considerable debate regarding the placement of *Penthorum*. Some have included this enigmatic genus in Saxifragaceae (Cronquist, 1981; Dahlgren, 1983), others in Crassulaceae (Hutchinson, 1973), and some recognize Penthoraceae (Takhtajan, 1987; Thorne, 1992). *Penthorum* has morphological characteristics of both Saxifragoideae and Crassulaceae and, depending on which features are emphasized, a case could be made for its alliance with either. In having a hypanthium, partially connate carpels, and nonsucculent leaves, *Penthorum* is more like Saxifragoideae. However, *Penthorum* is more similar to Crassulaceae in number of floral parts. Syncarpous gynoecia and shallow hypanthia in two crassulaceous genera (*Diamorpha* and *Triactinia*) also suggest a link between *Penthorum* and Crassulaceae.

*Penthorum* has been the subject of numerous systematic studies, but the results have for the most part been inconclusive. Hamel (1953) found that $n = 8$ and 9 in *Penthorum* and suggested that, since the same numbers were present in Saxifragoideae, it could be included there. Hideux & Ferguson (1976) found the complex, H-shaped endoapertures in the pollen exine of *Penthorum* to be much like those of *Sedum* (Crassulaceae), but in other pollen characteristics *Penthorum* appeared intermediate between Saxifragoideae and Crassulaceae. According to Jay (1970), *Penthorum* has more phenolic constituents in common with Saxifragoideae (notably ellagic acid) than with Crassulaceae. Soltis & Bohm (1982), however, found that *Penthorum* was chemically distinct from Saxifragoideae in containing many unique, unidentified flavonoids. Also, while myricetin and flavones are found in Saxifragoideae, they are absent in *Penthorum*.

Because Crassulaceae are a much more easily defined group without *Penthorum*, the genus is often allied with Saxifragoideae (Spongberg, 1972). The phylogenetic analysis of morphological and chemical data of Hufford (1992) suggests that *Penthorum* is more closely related to Saxifragoideae than to Crassulaceae. Similarly, Haskins & Hayden (1987) remarked that *Penthorum* does not possess the morphological characters that define Crassulaceae. However, in a detailed anatomical study, they found that *Penthorum* also shares no definite synapomorphies with Saxifragoideae; most of its distinguishing features are either plesiomorphic or of uncertain status. Finding no anatomical or morphological characters to place *Penthorum* in either Saxifragoideae or Crassulaceae, Haskins & Hayden suggested that the genus is most easily accommodated in its own family (Penthoraceae).

Our data also suggest that *Penthorum* should not be accommodated in either Saxifragoideae or Crassulaceae, although the genus is more closely related to Crassulaceae than to Saxifragoideae (Figs. 2, 3). The closest relative of *Penthorum* identified by *rbc*L sequence data is *Myriophyllum* (Haloragaceae). A close relationship between Haloragaceae and *Penthorum* or Crassulaceae has apparently never been suggested. Haloragaceae are occasionally placed in the order Haloragales, often with *Gunnera* (Cronquist, 1981; Dahlgren, 1983); the family is also often placed in the Myrtales (Hutchinson, 1973; Melchior, 1964a; Takhtajan, 1987). Haloragaceae are, however, distinguished from most families in Myrtales by several features, such as an aquatic habit, anemophily, reduced unisexual flowers, a partly apocarpous gynoecium, and a persistent, copious endosperm. Some of these fea-

tures (a partly apocarpous gynoecium and copious endosperm) are also found in *Penthorum*, *Tetracarpaea*, and Crassulaceae, the taxa most closely associated with *Myriophyllum* in our analysis. Furthermore, *Myriophyllum*, *Penthorum*, and Crassulaceae have bitegmic crassinucellate ovules and cellular endosperm formation (Table 2). This is a rather uncommon combination of characters, with bitegmic crassinucellate ovules more often being associated with nuclear endosperm development. This latter, more common combination is found in Myrtales (Dahlgren, 1975b; Davis, 1966; Philipson, 1974, 1977).

The *rbc*L-supported alliances are generally in agreement with the suggestion of Haskins & Hayden (1987) that *Penthorum* is perhaps most easily accommodated in its own family separate from both Saxifragaceae and Crassulaceae. The placement of *Penthorum* and *Myriophyllum* as sister taxa by sequence data, however, raises the new possibility of a close relationship between *Penthorum* and Haloragaceae. The embryological similarities between *Penthorum* and *Myriophyllum* are intriguing, and the relationship between these taxa should be investigated further. Sequence data for additional genera of Haloragaceae would be extremely helpful. Another potential avenue of inquiry would be to investigate the flavonoids in *Myriophyllum*. Soltis & Bohm (1982) found the most distinctive feature of *Penthorum* to be the presence of numerous unidentified flavonoids different from anything found in Saxifragaceae. Identification of these compounds in *Penthorum* and determination of whether they are present in Haloragaceae would be useful.

*Tetracarpaeoideae.* Tetracarpaeoideae consist only of the single shrubby species *Tetracarpaea tasmanica* Hook.f. Our *rbc*L results (Figs. 2, 3) indicate that *Tetracarpaea* is most closely allied with the herbaceous genera *Penthorum* and *Myriophyllum*, and only distantly related to most other woody taxa of Saxifragaceae *s. l.* This placement of *Tetracarpaea* does not parallel most classifications of the genus, which usually place it as a close ally of other woody taxa of Saxifragaceae *s. l.* (e.g., Hydrangeoideae, Escallonioideae, Montinioideae). The placement of *Tetracarpaea* suggested by *rbc*L evidence is, however, similar to the classification of Thorne (1992), who considered it to be more closely related to Saxifragoideae and other herbaceous taxa.

Although *Tetracarpaea* has usually been allied with other woody taxa of Saxifragaceae *s. l.*, there have nonetheless been indications that the true alliances of this genus lie elsewhere. Hideux & Ferguson (1976) suggested that, based on overall pollen characteristics, *Tetracarpaea* is most closely related to Cunoniaceae, a woody family of Rosidae. Hils et al. (1988), however, discounted such a relationship because of floral morphology. Furthermore, in exine characteristics alone, the pollen of *Tetracarpaea* is different from that of Cunoniaceae, and also unlike that of most other woody taxa of Saxifragaceae *s. l. Tetracarpaea* appears most similar in pollen exine features to *Tellima* and *Astilboides*, genera of Saxifragoideae (Hideux & Ferguson, 1976).

Hils et al. (1988) revealed that, although the wood anatomy of *Tetracarpaea* was similar to that of other woody Saxifragaceae *s. l.*, the vascular anatomy of the nodes, leaves, and floral parts of *Tetracarpaea* was different from that of woody Saxifragaceae *s. l.* In addition, whereas the ovules in many other woody members of Saxifragaceae *s. l.* are unitegmic and tenuinucellate, in *Tetracarpaea* they are identical to Saxifragoideae and Crassulaceae in being bitegmic and crassinucellate (Table 2). The closer relationship of *Tetracarpaea* to Saxifragoideae than to other woody Saxifragaceae *s. l.* suggested by embryological, anatomical, and morphological studies is corroborated by *rbc*L sequence data (Figs. 1–3).

Some features of *Tetracarpaea* (e.g., hypogynous flowers with completely separate carpels) are distinctly like those of Crassulaceae, and *rbc*L sequence data also provide support for a closer relationship of this genus to Crassulaceae than to Saxifragoideae. *Tetracarpaea* has not, however, been considered most closely related to *Penthorum* or *Myriophyllum*. Further investigation of the entire *rbc*L-supported *Tetracarpaea–Penthorum–Myriophyllum* alliance is in order. One possible course is to extend the identification of the many unknown flavonoids found in *Penthorum* (see above) to *Tetracarpaea* and *Myriophyllum*. Myricetin, which is found in both Saxifragoideae and Crassulaceae, is absent in *Penthorum* (Gornall et al., 1979; Soltis & Bohm, 1982), and its presence or absence should be confirmed in *Tetracarpaea* and Haloragaceae. Flavones are also found in Saxifragoideae and Crassulaceae but are absent in *Penthorum* and are not yet known in Haloragaceae (Gornall et al., 1979; Soltis & Bohm, 1982). In addition, endosperm development, although known for *Penthorum* and Crassulaceae, has apparently not been determined for *Tetracarpaea* and several members of Haloragaceae and Haloragales.

### III. SUBFAMILIES ASSOCIATED WITH OTHER FAMILIES OF ROSIDAE

*Baueroideae.* Except for Engler (1890, 1928), Schulze-Menz (1964), and Hutchinson (1973), most workers have considered *Bauera* to be distinct from all other constituents of Saxifragaceae *s. l.* and more closely related to, or included in, Cunoniaceae. Sequence data of *rbc*L are in complete agreement with a close relationship between *Bauera* and Cunoniaceae and a distant relationship between *Bauera* and all other members of Saxifragaceae *s. l.* (Figs. 2, 4). In supporting the alliance of *Bauera* with *Ceratopetalum* (Cunoniaceae), our data corroborate many other lines of evidence.

Some fairly obvious morphological features shared by *Bauera* and Cunoniaceae that are rare or absent in most other members of Saxifragaceae *s. l.* are compound leaves and numerous stamens. Bensel & Palser (1975d) advocated a close relationship between *Bauera* and Cunoniaceae because of similarities in floral anatomy. Among other features, they found that sepal-plane vascular bundles do not contribute to either androecial or gynoecial vasculature in *Bauera*, whereas they do in many other taxa of Saxifragaceae *s. l.*

The ovules in *Bauera*, Cunoniaceae, Saxifragoideae, and the subfamilies of Saxifragaceae *s. l.* already discussed here are bitegmic and crassinucellate. Whereas endosperm formation in Saxifragoideae and allied subfamilies (e.g., Ribesoideae, Penthoroideae) is cellular or helobial, in *Bauera* and Cunoniaceae it is nuclear (Table 2). In fact, only one other subfamily of Saxifragaceae *s. l.* (Francooideae) is known to have the same three embryological features (Table 2). Also, both *Bauera* and Cunoniaceae have a zigzag micropyle, whereas all other members of Saxifragaceae *s. l.* have more typical straight micropyles (Davis, 1966). Prakash & McAlister (1977) cited many embryological and seed characteristics that were similar in *Bauera* and Cunoniaceae but markedly different in other members of Saxifragaceae *s. l.*

*Bauera* is also palynologically similar to Cunoniaceae. Erdtman (1966) reported the pollen of *Bauera* and Cunoniaceae to be similar in being two-colpate and approximately half as large as the pollen of Saxifragoideae. Hideux & Ferguson (1976) described exine features and results of a numerical analysis of many pollen characters that also indicated a close *Bauera*–Cunoniaceae relationship. Similarities in secondary chemicals also indicate a relationship between *Bauera* and Cunoniaceae (Jay, 1970). Recent phylogenetic analyses of morphological, anatomical, and chemical characters (Hufford, 1992; Hufford & Dickison, 1992) indicate that *Bauera* should be included within Cunoniaceae.

In recent years it has rarely been suggested that *Bauera* is more closely related to other members of Saxifragaceae *s. l.* than to Cunoniaceae. Dickison (1975) described vegetative patterns, anther dehiscence, and flower vestiture features that distinguished *Bauera* from Cunoniaceae and suggested that *Bauera* was closer to Saxifragoideae than to Cunoniaceae. Nearly all other evidence, however, including *rbc*L sequence data, strongly suggests that *Bauera* should be included within or closely allied with Cunoniaceae.

*Eucryphia*, the only genus in Eucryphiaceae, is also a close relative of *Bauera* and Cunoniaceae in our results (Figs. 2, 4). *Eucryphia* is a genus of shrubs and trees that, like Cunoniaceae and *Bauera*, is distributed in the Southern Hemisphere. Focke (1895) and Melchior (1964b) placed *Eucryphia* near Dilleniaceae and Ochnaceae, but most recent workers consider it closely related to or part of Cunoniaceae (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1987; Thorne, 1992). Evidence from flavonoids (Bate-Smith et al., 1967) and cytology (Hamel, 1959) supports a close relationship between Eucryphiaceae and Cunoniaceae. More recently, investigations of floral, leaf, and wood anatomy (Dickison, 1978) and pollen features (Hideux & Ferguson, 1976) have also supported a close relationship between the two families. Hufford (1992) and Hufford & Dickison (1992) performed phylogenetic analyses of morphological, anatomical, and chemical characters, finding that *Eucryphia* is very closely related to and possibly should be included in Cunoniaceae. Our *rbc*L sequence data, therefore, correlate well with several lines of evidence in supporting a close alliance between *Eucryphia* and Cunoniaceae.

*Francooideae.* Our *rbc*L sequence data suggest that *Francoa* (one of two genera in the subfamily) is distantly related to Saxifragoideae and all other members of Saxifragaceae *s. l.*, and closely related to *Greyia* (Greyiaceae; Figs. 2, 4). In most classifications Francooideae has been closely allied with Saxifragoideae, either as part of a narrowly defined Saxifragaceae (Cronquist, 1981; Dahlgren, 1983) or as a closely related family (Hutchinson, 1973; Takhtajan, 1987; Thorne, 1992).

Some evidence indicates a close relationship between Francooideae and Saxifragoideae. Bensel & Palser (1975b) found the floral anatomy of *Fran-*

*coa* to be very much like that of other genera in Saxifragoideae. Hamel (1953) reported the chromosome number of *Francoa sonchifolia* Cav. to be $n = 26$ and suggested a close relationship between *Francoa* and Saxifragoideae because the same number also occurs in Saxifragoideae, although rarely. Jay (1970) also suggested that *Francoa* and Saxifragoideae were closely related, based on the shared occurrence of ellagic acid.

Other evidence parallels *rbc*L sequence data in suggesting a distant relationship between *Francoa* and Saxifragoideae. Bohm et al. (1986) identified several flavonoids in *Francoa* (e.g., quercetin and kaempferol aglycones) that had not been reported for this genus by Jay (1970). They also found myricetin and rutinosides, compounds commonly found in Saxifragoideae, to be absent in *Francoa*. Bohm et al. (1986) concluded, in contrast to Jay (1970), that *Francoa* was distinct from Saxifragoideae and should be recognized as a separate family. Hideux & Ferguson (1976) found the complex apertures of both genera in Francooideae (*Francoa* and *Tetilla*) to be different from the diffuse and simple endoapertures of Saxifragoideae. Their numerical analysis of 25 pollen characters also separated *Francoa* and *Tetilla* from Saxifragoideae.

Our sequence data indicate that the closest relative of *Francoa* is *Greyia* (Figs. 2, 4). Greyiaceae have been allied with or included in Melianthaceae by some authors (e.g., Scholz, 1964). *Greyia* is, however, distinguished from Melianthaceae by several morphological and chemical features (Bohm & Chan, 1992), and recently the family has been included in the same order or suborder as Saxifragaceae (Cronquist, 1981; Dahlgren, 1983; Takhtajan, 1987; Thorne, 1992). It has, however, never been thought to be closely related to *Francoa*.

Although a close relationship between *Francoa* and *Greyia* may initially seem anomalous, other data do corroborate our *rbc*L results. Myricetin, while common in Saxifragoideae, is absent in both *Francoa* (Bohm et al., 1986) and *Greyia* (Gornall et al., 1979). According to Erdtman (1966), the pollen of *Francoa* is quite different from Saxifragoideae, having an equatorial constriction. Hideux & Ferguson (1976) revealed that the pollen of both genera of Francooideae is very similar to that of *Greyia*. There are also floral characters that distinguish *Francoa* from Saxifragoideae and support its relationship with *Greyia*. Whereas most Saxifragoideae have two carpels, *Francoa* has four (*Greyia* has five). Staminodes are not known in Saxifragoideae, but *Francoa* and *Greyia* both possess staminodes equal in number to fertile stamens. Finally, in both *Francoa* and *Greyia* endosperm formation is initially nuclear, whereas Saxifragoideae (as well as Crassulaceae and other taxa related to Saxifragoideae) have cellular (or sometimes helobial) endosperm formation (Table 2).

The results of *rbc*L sequence analysis also suggest that there is an alliance between the *Francoa–Greyia* group and *Viviania*, although support for this relationship is low (Figs. 2, 4). *Viviania*, which has been either included in Geraniaceae or recognized as a separate, monogeneric family, is poorly known chemically and embryologically. At this time we cannot, therefore, provide useful comparisons between this *rbc*L-supported alliance and other lines of evidence; the possible relationship between *Viviania* and *Greyia–Francoa* must be investigated further.

*Brexioideae.* The *rbc*L sequence data suggest a close alliance between *Brexia* (one of three genera of Brexioideae) and *Euonymus* (Celastraceae), separating *Brexia* from Saxifragoideae and most other members of Saxifragaceae *s. l.* (Figs. 2, 4). *Brexia* has typically been associated with Escallonioideae and other woody subfamilies of Saxifragaceae *s. l.* (Cronquist, 1981; Engler, 1890, 1928; Hutchinson, 1973; Thorne, 1992). Dahlgren (1983), however, allied *Brexia* more closely with a narrowly defined Saxifragaceae than with Escallonioideae. Takhtajan (1987) placed Brexiaceae with Celastraceae (in Celastrales).

The relationships of *Brexia* have been difficult to ascertain because different characters unite the genus with different groups of plants. Some evidence appears to unite *Brexia* with other woody Saxifragaceae *s. l.*, especially Escallonioideae. As noted above, Jay (1970) interpreted flavonoid data to support a close relationship between *Itea*, *Brexia*, and *Escallonia*. Pollen exine characteristics of *Brexia* (Hideux & Ferguson, 1976) are most similar to those of *Argophyllum* (Escallonioideae). A numerical analysis of many more pollen characters also supported inclusion of *Brexia* in a broadly defined Escalloniaceae, containing such additional taxa as *Itea* and *Tetracarpaea* (Hideux & Ferguson, 1976). Plouvier (1965) not only supported a *Brexia–Itea* relationship but also suggested a relationship between *Brexia* and Celastraceae because both produce dulcitol.

*Brexia* differs from both Saxifragoideae and Escallonioideae in floral morphology and anatomy. Bensel & Palser (1975a) provided a long list of floral features present in *Brexia* and absent or rare in either or both Saxifragoideae and Escallonioideae, including a completely superior ovary, five

carpels, isomerous flowers, completely connate carpels, staminodes, anther extensions, thick carpel walls, and evidence that the androecium was derived from fascicled stamens. However, because *Brexia* differed more substantially from other members of Saxifragaceae *s. l.*, Bensel & Palser (1975d) tentatively allied the genus with Escallonioideae, pending further investigation.

The close relationship between *Brexia* and *Euonymus* suggested by *rbc*L sequence data corroborates the placement of *Brexia* in Celastrales by Takhtajan (1987) and the suggestion that *Brexia* and Celastraceae are closely related based on chemical evidence (Plouvier, 1965). The five-carpellate, isomerous flowers with superior ovaries found in *Brexia* also characterize *Euonymus*. In addition, the ovules in most taxa of Saxifragaceae *s. l.* are either bitegmic and crassinucellate or unitegmic and tenuinucellate. *Brexia*, however, has bitegmic and tenuinucellate ovules, as does *Euonymus*. Many members of Saxifragaceae *s. l.* also have cellular endosperm formation; in contrast, *Brexia* and *Euonymus* have nuclear endosperm formation (Table 2). The combination of these three embryological characteristics is relatively uncommon not only in Saxifragaceae *s. l.*, but also in dicots in general (Dahlgren, 1975b; Philipson, 1974, 1977). Thus, embryological data further support a close relationship between *Brexia* and *Euonymus*.

Although *rbc*L sequence data and embryological evidence suggest a close relationship between *Brexia* and *Euonymus*, inclusion of *Brexia* in Celastraceae would be premature at this time. *Euonymus* may not be typical of Celastraceae or Celastrales. Some taxa in Celastraceae (e.g., *Celastrus*) have crassinucellate ovules (Davis, 1966), and in other characteristics the family is a very diverse group (Cronquist, 1981). Other families in Celastrales (sensu Cronquist) are also different from *Euonymus* embryologically, and the only other one for which *rbc*L sequences are available (Aquifoliaceae) is, according to *rbc*L evidence, very distantly related to *Euonymus* (Figs. 1, 5; see below). Because basic chemical data for *Brexia* are lacking, no insights into the relationships of this genus can presently be gained through comparative chemistry. It is noteworthy that Celastraceae possess a rare flavonoid type (5-deoxy flavonoids, Gornall et al., 1979). It would, therefore, be of interest to determine whether these compounds are also present in *Brexia*. Further resolution of the potential *Brexia* Celastrales alliance should await further chemical and molecular investigation of Celastrales.

*Parnassioideae and Lepuropetaloideae.* Our *rbc*L sequence evidence indicates a close relationship between *Parnassia* and *Lepuropetalon* (Figs. 2, 4). These two genera were initially allied as subfamily Parnassioideae of Saxifragaceae (Dandy, 1927). Most recent classifications consider them closely related to one another; many authors retain them in narrowly defined versions of Saxifragaceae (Cronquist, 1981; Dahlgren, 1983; Hutchinson, 1973) or in separate families in the same order (Takhtajan, 1987; Thorne, 1992). Dahlgren (1983), although allying the two genera, included them in Droserales (as the families Parnassiaceae and Lepuropetalaceae) rather than in Saxifragales.

*Parnassia* and *Lepuropetalon* share many morphological characteristics, such as a dimorphic androecium with staminodes, similar epidermal tannin sacs, commisural stigmas, loculicidal capsules, and a scanty endosperm (Spongberg, 1972). Gastony & Soltis (1977) obtained a chromosome count of $2n = 46$ for *Lepuropetalon* and established that two base chromosome numbers occur in *Parnassia* ($x = 8, 9$). Because of the dramatic difference in diploid numbers between *Parnassia* and *Lepuropetalon*, they did not consider cytological data to either confirm or deny a close relationship between the two. The complex mixtures of quercetin and kaempferol derivatives discovered in *Parnassia* by Bohm et al. (1986) clearly distinguish this genus from Saxifragoideae. Bohm et al. (1986) also found that the flavonoid constitution of *Lepuropetalon* was more similar to *Parnassia* than to any other investigated taxa of Saxifragaceae *s. l.* In pollen exine features, *Parnassia* and *Lepuropetalon* are much alike, with partial, continuous, and reticulate exines and similar endo- and ectoapertures. A numerical analysis involving many additional pollen characters did not, however, place the two close together (Hideux & Ferguson, 1976).

*Parnassia* is the better known of the two genera. Although *Parnassia* has been closely allied with Saxifragoideae in many classification schemes (Table 1), many lines of evidence do not support such a relationship. Jay (1970) claimed to have found support from flavonoids for allying *Parnassia* with Hypericaceae. In contrast, Hamel (1953) preferred to ally *Parnassia* very closely with Saxifragoideae because of similar karyotypes and because the chromosome numbers reported for *Parnassia* at that time ($2n = 16$ and 32) were also present in Saxifragoideae.

Bensel & Palser (1975a) found, however, that *Parnassia* shared very few floral characteristics with Saxifragoideae and proposed treating it as a separate family. They described *Parnassia* as hav-

ing hypogynous flowers, completely connate ovaries, mostly commissural stigmas, nectariferous staminodia, and an ancestrally fascicled androecium; all of these features are absent or rare in Saxifragoideae. Grund & Jensen (1981), in a serological investigation of seed antigens of *Parnassia*, detected no reactions with either *Saxifraga* or *Hydrangea*, suggesting distant relationships with both (they did not, however, investigate *Lepuropetalon*). *Parnassia* is also embryologically different from Saxifragoideae. It has bitegmic tenuinucellate ovules and nuclear endosperm formation, whereas bitegmic crassinucellate ovules and cellular endosperm characterize Saxifragoideae (Table 2). Thus, our *rbc*L sequence data are in agreement with several lines of biosystematic data in supporting a close relationship between *Parnassia* and *Lepuropetalon* and a distant relationship between both genera and Saxifragoideae (Figs. 2, 4).

*Parnassia* and *Lepuropetalon* are part of a well-supported clade based on *rbc*L sequence data that also contains *Brexia* and *Euonymus* (Figs. 2, 4). It is important to note that other lines of evidence suggest a close alliance among all the members of the group. The combination of embryological features found in *Brexia*, *Euonymus*, and *Parnassia* is found commonly only in Ebenales, Theales, and Primulales (Dahlgren, 1975b; Philipson, 1974, 1977; Table 2). *Brexia*, *Parnassia*, and *Lepuropetalon* also possess staminodes and, as noted by Bensel & Palser (1975a), *Brexia* and *Parnassia* are similar in having an ancestral fascicled androecium, with several small vascular bundles supplying each stamen. The diminutive *Lepuropetalon*, considered the smallest terrestrial angiosperm, is not well known in most respects. Schulze-Menz (1964) reported it as having unitegmic ovules, in which it would differ from *Parnassia* and *Brexia*. This should be confirmed, however, and the nucellus and endosperm types of *Lepuropetalon* should also be determined. A better knowledge of *Lepuropetalon* as well as of other taxa in Celastraceae should add significantly to an understanding of this alliance.

## IV. SUBFAMILIES ASSOCIATED WITH CORNACEAE

*Hydrangeoideae.* Our analysis of *rbc*L sequence data indicates that the closest relatives of Hydrangeoideae are Cornaceae and related genera (Fig. 5). There have been long-standing disagreements regarding the proper placement of the genera of Hydrangeoideae (see Table 1). Whereas Schulze-Menz (1964) and Cronquist (1981) preferred a relatively close relationship between this group of genera and Saxifragoideae, Hutchinson (1973), Dahlgren (1983), Takhtajan (1987), and Thorne (1992) allied the group (along with other woody subfamilies) with taxa that are distantly related to Saxifragoideae, such as Cornaceae or Cunoniaceae. It is significant, therefore, that *rbc*L sequence data suggest that the five genera of Hydrangeoideae analyzed are allied with Cornaceae, in agreement with the relationships suggested by Huber (1963), Dahlgren (1983), Takhtajan (1987), and Thorne (1992).

Most recent evidence has made it apparent that Hydrangeoideae are only distantly related to Saxifragoideae. Bate-Smith (1962) reported that ellagic acid was present in Saxifragoideae, but absent in Hydrangeoideae, suggesting that the two were distantly related. Jay (1970) found the same distribution of ellagic acid but concluded that Hydrangeoideae were less distantly related to Saxifragoideae. Perhaps the first to draw attention to similarities between Hydrangeoideae and Cornales was Huber (1963), who cited such shared features as scalariform perforations in the xylem and the absence of stipules and recommended placing Hydrangeoideae within Cornales.

Bensel & Palser (1975c, d) found several anatomical characteristics that distinguished Hydrangeoideae from Saxifragoideae, such as an increase in stamen numbers, highly vascularized gynoecia, absence of hypanthia, and three-trace petals with some bundles originating from the sepal planes. Krach (1977) also decided that several characteristics of Hydrangeoideae, such as a septicidal capsule, numerous seeds, reduced embryo size, and a lengthening of cell walls of the outer seed coat, indicated a distant relationship with Saxifragoideae. Palynological data also distinguish Hydrangeoideae from Saxifragoideae. Erdtman (1966) described the pollen of *Philadelphus* as being half as large as the pollen of Saxifragoideae. Hideux & Ferguson (1976) found several genera of Hydrangeoideae to be remarkably similar in exine characteristics. Their numerical analysis of additional pollen characters also indicated that Hydrangeoideae are homogeneous and well separated from Saxifragoideae.

Although the investigations discussed above all found characteristics that distinguished Hydrangeoideae from Saxifragoideae, few (e.g., Huber, 1963) proposed alternative relationships for the hydrangeoids. Grund & Jensen (1981) found that genera of Hydrangeoideae had a higher serological affinity with *Cornus* than with any of the numerous other samples tested, including *Escallonia*, *Ribes*, *Parnassia*, and representatives of Byblidaceae, Ericaceae, Caprifoliaceae, Crassulaceae, and Cunoniaceae. Significantly, they reported a low affinity

between Hydrangeoideae and several generea of Saxifragoideae. Thus, serological data clearly support Huber's contention that Hydrangeoideae are phylogenetically distant from Saxifragoideae and closely related to Cornaceae.

Additional support for a close relationship between Hydrangeoideae and Cornaceae comes from investigations of secondary chemicals, iridoids in particular. Iridoids occur primarily in sympetalous taxa, such as Dipsacales, Goodeniales, Oleales, Gentianales, Scrophulariales, and Lamiales. They also occur in Cornaceae, as well as genera often considered allied with Cornaceae (e.g., *Alangium*, *Aucuba*, *Curtisia*, *Davidia*, *Nyssa*). Significantly, iridoids have also been found in *Deutzia*, *Fendlera*, and *Hydrangea* of Hydrangeoideae (Dahlgren et al., 1981; Jensen et al., 1975; Kaplan & Gottlieb, 1982). The presence of iridoids in Hydrangeoideae, coupled with their absence in Saxifragoideae and many other taxa of Saxifragaceae *s. l.*, indicate that Hydrangeoideae are more closely allied with Cornaceae and other iridoid-producing groups than with Saxifragoideae or other members of Saxifragaceae *s. l.* Similar alliances are suggested by flavonoid data. Whereas myricetin is common in Saxifragoideae, it is rare or absent in both Hydrangeoideae and Cornaceae (Bohm et al., 1985; Gornall et al., 1979).

Most of the plant groups containing iridoids also have ovules that are unitegmic and tenuinucellate. The ovules of Hydrangeoideae are also unitegmic and tenuinucellate, distinct from the bitegmic and crassinucellate ovules of Saxifragoideae. Although some of the cornalean taxa in this analysis differ from Hydrangeoideae in having crassinucellate ovules, all have ovules that are unitegmic and most have cellular endosperm formation (Dahlgren, 1975b; Davis, 1966). Recently, Hufford (1992) presented results from a phylogenetic analysis of many morphological, anatomical, and chemical characters that supported an alliance between Hydrangeoideae and Cornales. In summary, *rbc*L evidence, in combination with chemical, embryological, morphological, and anatomical characteristics, strongly supports the separation of Hydrangeoideae from Saxifragoideae and indicates that they are probably most closely related to Cornales. The Hydrangeoideae–Cornaceae relationship is the subject of a more detailed *rbc*L sequence analysis by Xiang et al. (1993).

## V. SUBFAMILIES ASSOCIATED WITH ASTERIDAE

*Phyllonomoideae.* *Phyllonoma*, the only genus in the subfamily, is not, according to *rbc*L sequence evidence, closely allied with any other members of Saxifragaceae *s. l.* Rather, it is part of an alliance that is composed primarily of sympetalous taxa usually placed in Asteridae (Fig. 5). Members of this asterid group almost exclusively have ovules that are unitegmic and tenuinucellate (Dahlgen, 1975b; Davis, 1966), and many of them produce iridoid compounds (Fig. 5).

*Phyllonoma* is included in this group as a relative of *Helwingia* and *Ilex* (Fig. 5). *Helwingia* is usually included within Cornales (a detailed discussion of Cornaceae and related taxa is provided by Xiang et al., 1993). *Ilex* (Aquifoliaceae), although it has also been associated with Cornales (Dahlgren, 1983), is most often included in Celastrales. Our analysis of *rbc*L sequence data indicates, however, that both *Helwingia* and *Ilex* are far removed phylogenetically from the groups with which they have traditionally been allied.

Most authors have placed Phyllonomoideae with other woody members of Saxifragaceae *s. l.* The genus has frequently been considered most closely related to Escallonioideae (Table 1), but its placement is often described as uncertain. Compared with most other subfamilies of Saxifragaceae *s. l.*, Phyllonomoideae are poorly known; very little embryological, anatomical, or chemical evidence has been obtained. Palynological data are available, however, and Erdtman (1966) and Hideux & Ferguson (1976) found the pollen of *Phyllonoma* to differ from that of other saxifragaceous taxa. The combination of a complete, granulate tectum and a simple endoaperture in *Phyllonoma* was unlike the pollen of any other subfamily of Saxifragaceae *s. l.* Hideux & Ferguson (1976) also found that, based on many additional pollen features, *Phyllonoma* could not easily be accommodated in any saxifragaceous group and differed most from Escallonioideae and Hydrangeoideae. In contrast to pollen characters, seed coat features suggest that *Phyllonoma* is closely related to *Ribes* (Krach, 1977). In a revision of *Phyllonoma*, Mori & Kallunki (1977) discussed its generic relationships only briefly but also suggested that it was closely related to *Ribes*.

*Phyllonoma* has never been closely associated with *Ilex*, and it has only indirectly been associated with *Helwingia*. Nonetheless, there is evidence that corroborates the relationships suggested by *rbc*L sequence data. All three of these genera have separate petals, a feature that distinguishes them in this group of mostly sympetalous taxa. Evidence supporting the alliance of *Phyllonoma* and *Helwingia* is provided by leaf morphology and inflorescence features. Hickey & Wolfe (1975) noted that the leaves of the two genera have derived brochidodromous venation, possibly because they

share a common ancestor. Perhaps the most intriguing evidence linking *Phyllonoma* and *Helwingia* is the fact that both genera have inflorescences borne on the upper surfaces of the leaves. Besides *Phyllonoma* and *Helwingia*, epiphyllous inflorescences are found in at least 43 other genera in 24 families (Johnson, 1958; Dickinson, 1978). Most are assumed to have arisen by adnation of peduncles and petioles. Because various degrees of adnation can be found in individual families or genera, this characteristic has not been thought to be useful for phylogenetic purposes. Not all epiphyllous inflorescences are ontogenetically identical, however. Several taxa with this feature have been studied in detail. In some, the epiphyllous inflorescences have arisen from peduncle–petiole adnation: Dichapetalaceae (Stork, 1956), *Chirita* (Gesneriaceae; Johnson, 1958), and *Turnera* (Turneraceae; Johnson, 1958). The epiphyllous inflorescences of *Phyllonoma* and *Helwingia* are, however, ontogenetically different from others that have been studied because they arise from the upper surfaces of the leaf primordia (Dickinson & Sattler, 1974, 1975; Johnson, 1958). This shared characteristic adds considerable support to the alliance of *Phyllonoma* and *Helwingia*.

Additional evidence relevant to the *Phyllonoma–Helwingia–Ilex* relationship may come from secondary chemicals, chromosome data, and embryological features. *Phyllonoma*, *Helwingia*, and *Ilex* comprise one of several lineages in this primarily asterid alliance in which iridoids have not been found (Fig. 5). *Helwingia* and *Ilex* are not known to produce iridoids (Dahlgren, 1983; Dahlgren et al., 1981) but *Phyllonoma* has not been tested for iridoids. It would, therefore, be of value to determine whether *Phyllonoma* possesses iridoid compounds. The chromosome numbers of *Helwingia* ($x = 19$) and *Ilex* ($x = 20$) are similar (Raven, 1975); a chromosome count for *Phyllonoma* should also be useful. *Ilex* and most members of Aquifoliaceae have unitegmic and crassinucellate ovules, a relatively uncommon combination (Dahlgren, 1975b; Philipson, 1974, 1977). *Phyllonoma* and *Helwingia* have also been reported to have unitegmic ovules (Schulze-Menz, 1964), but their nucellar type is unknown. A finding of crassinucellate ovules in *Phyllonoma* and *Helwingia* should provide further support for this alliance.

*Escallonioideae.* As with *Phyllonoma*, *rbc*L sequence analysis places *Escallonia* in an alliance of asterid taxa (Fig. 5). Escallonioideae have most often been associated with the woody subfamilies Hydrangeoideae and Montinioideae (Table 1). Our *rbc*L sequence data indicate, however, that *Escallonia* is well separated from both. Although clearly separating *Escallonia* from all other members of Saxifragaceae *s. l.*, *rbc*L sequence data provide little support for a close alliance of the genus with any other lineage (Fig. 5).

Escallonioideae are the most morphologically diverse of the 17 subfamilies of Saxifragaceae *s. l.*, and appears to be polyphyletic. There is no consensus concerning the composition of the subfamily; several genera that have been placed in Escallonioideae (e.g., *Corokia*, *Griselinia*) have also been associated with families such as Cornaceae and Araliaceae (Eyde, 1966; Philipson, 1967).

The morphological diversity encountered within Escallonioideae has complicated attempts to determine the relationships of the group. Bensel & Palser (1975c) studied five members of Escallonioideae (*Corokia*, *Carpodetus*, *Quintinia*, *Escallonia*, and *Polyosma*) and described them as being very diverse in floral morphology and floral vascular patterns. Similarly, Hideux & Ferguson (1976) discovered that pollen morphology among genera of the subfamily was so diverse that several other subfamilies of Saxifragaceae *s. l.* could easily be accommodated within the variation.

Other evidence indicates considerable evolutionary distance between Escallonioideae and Saxifragoideae. Serological affinities of *Escallonia* are much higher with *Roridula*, *Sambucus*, *Lonicera*, *Cornus*, and Hydrangeoideae than with Saxifragoideae (Grund & Jensen, 1981). Several other features distinguish Escallonioideae from Saxifragoideae; in many instances Escallonioideae are much like Hydrangeoideae. In seed characteristics Escallonioideae and Hydrangeoideae are similar, and both groups differ from Saxifragoideae (Krach, 1977). Ellagic acid is absent from both Escallonioideae and Hydrangeoideae but present in Saxifragoideae (Bate-Smith, 1962; Jay, 1970). Iridoids are present in Escallonioideae and Hydrangeoideae but absent in Saxifragoideae (Dahlgren et al., 1981; Jensen et al., 1975; Kaplan & Gottlieb, 1982). Both Escallonioideae and Hydrangeoideae also have unitegmic, tenuinucellate ovules (Table 2).

Our *rbc*L sequence data agree in part with the above described lines of evidence by indicating that *Escallonia* is phylogenetically distant from Saxifragoideae and closely related to other taxa that produce iridoids and that have unitegmic (and usually tenuinucellate) ovules. The closest allies of *Escallonia* are not, however, Hydrangeoideae and Cornaceae (Fig. 5). There are, in fact, embryological and morphological features that parallel *rbc*L evidence in distinguishing *Escallonia* from Hydrangeoideae and/or Cornaceae. Endosperm formation is nuclear in Escallonioideae but cellular in

Hydrangeoideae and Cornaceae. Whereas ovules in Cornaceae are mostly crassinucellate, in *Escallonia* and other genera of Escallonioideae they are tenuinucellate (Table 2). Genera of Escallonioideae are also distinguished from Hydrangeoideae and Cornaceae by exhibiting haplostemonous and sympetalous tendencies (Dahlgren, 1983); these characteristics also are consistent with the placement of *Escallonia* with taxa of Asteridae.

Further resolution of the relationships of *Escallonia* is not possible at present with available *rbc*L sequence data because of the lack of evidence supporting specific alliances (Fig. 5). Given the great morphological diversity present in Escallonioideae and the poor understanding of generic relationships in the group, it will be necessary to investigate additional genera to gain a complete understanding of the systematics of the entire subfamily. Our *rbc*L sequence data have already been helpful in exploring the relationships of two genera, *Corokia* and *Griselinia*, that have been placed in Escallonioideae by some authors. Sequence data indicate that *Corokia* and *Griselinia* are not closely related to *Escallonia* or to one another (Fig. 5). It should be possible to gain a better understanding of Escallonioideae by obtaining *rbc*L sequence data from other members of the subfamily.

*Montinioideae.* *Montinia* represents still another member of Saxifragaceae *s. l.* whose affinities appear to be with taxa of Asteridae. The closest relatives of *Montinia*, according to *rbc*L sequence evidence, are Convolvulaceae and Solanaceae (Fig. 5), both of which are normally placed in Solanales (Asteridae).

Montinioideae (consisting of the two genera *Montinia* and *Grevea*) have been allied with many different taxa (e.g., Myrtaceae, Celastraceae, Cucurbitaceae, Onagraceae; see Dahlgren et al., 1977). The subfamily is most commonly allied, however, with other members of Saxifragaceae *s. l.*, especially the woody subfamilies Hydrangeoideae and Escallonioideae (Table 1). Montinioideae share several features with Hydrangeoideae and Escallonioideae that are not characteristic of many other members of Saxifragaceae *s. l.* All three subfamilies have unitegmic tenuinucellate ovules (Table 2), lack ellagic acid (Bate-Smith, 1962; Jay, 1970), and produce iridoids (Dahlgren et al., 1977, 1981; Jensen et al., 1977; Kaplan & Gottlieb, 1982).

According to *rbc*L sequence data, however, *Montinia* does not have Hydrangeoideae or Escallonioideae as closest relatives, although all three subfamilies do appear near members of Asteridae. Importantly, some more traditional lines of systematic data also do not closely link Montinioideae with Hydrangeoideae or Escallonioideae. Krach (1976) found many differences between the seeds of Montinioideae and Escallonioideae and suggested that they were distantly related. Takhtajan (1980) stated that some characteristics of Montinioideae (e.g., simple perforation plates in the xylem, unisexual flowers) indicate that they are much more advanced than either Hydrangeoideae or Escallonioideae.

Some morphological and anatomical features of *Montinia* are also present in Solanales. Both Montinioideae and Solanales have two-carpellate gynoecia and simple perforation plates in their xylem. Montinioideae are dioecious and have capsular fruits; dioecy (Levine & Anderson, 1986) and capsular fruits also occur in Solanales. Most of these shared morphological and anatomical features are, however, also found in many other taxa. Numerous features distinguish *Montinia* from Solanales; we will mention only the most obvious. In contrast to both Solanaceae and Convolvulaceae, *Montinia* has inferior ovaries, free stamens, separate petals, produces iridoids and lacks internal phloem.

Further study of Montinioideae should be useful in determining the closest relatives of this subfamily. For example, secondary chemical data may be helpful. According to Harborne & Swain (1979), Solanaceae have a unique flavonoid composition that is similar only to that of Convolvulaceae and Nolanaceae (also in Solanales). Specific chemical features shared by Solanaceae and Convolvulaceae include the presence of tropane alkaloids, otherwise known from only ten genera of six other families (Evans, 1979), and acylated anthocyanins, elsewhere found only in Lamiaceae and Polemoniaceae (Harborne & Swain, 1979). It would be useful to analyze *Montinia* for tropane alkaloids and acylated anthocyanins. In addition, Dahlgren et al. (1977) described an unusual condition in *Montinia* in which the cotyledon petioles of the seedlings are fused. This characteristic is rare in flowering plants and is almost exclusively found in herbaceous taxa. It has been described in other woody plants only in *Combretum* (Combretaceae) and in one species of *Quercus* (Fagaceae). In herbaceous taxa, fused petioles are known in four genera each of Ranunculaceae and Apiaceae and in one genus in each of three other families (de Vogel, 1980). Lubbock (1892) reported no occurrences of fused petioles in Solanales, but a more thorough examination of seedling development of Solanales might provide useful insights.

As noted by Chase et al. (1993), the misidentification of plant material should be considered a possibility, especially when relationships seem anomalous. It is significant, therefore, that our *rbc*L

sequence for a second specimen of *Montinia* confirms the results presented here.

*Vahlioideae.* According to *rbc*L sequence data, *Vahlia* (the only genus of Vahlioideae) is well separated from other members of Saxifragaceae *s. l.* and included in the same group of asterid families that contains *Montinia* (Fig. 5). Its inclusion in this group is well supported by *rbc*L sequence data. The results do not, however, indicate any close relatives for *Vahlia* in this alliance, but suggest that it is basal to several asterid taxa (Fig. 5).

*Vahlia* typically has been affiliated with other herbaceous taxa of Saxifragaceae *s. l.* (Table 1), either as a subfamily of Saxifragaceae or as a closely related family. As with *Pterostemon* and *Phyllonoma, Vahlia* is very poorly known anatomically and chemically, and although it is usually placed close to Saxifragoideae, its affinities are much in doubt. Embryological and palynological characteristics suggest that *Vahlia* is most closely related to *Parnassia.* Ovules in both genera are bitegmic and tenuinucellate (Table 2), indicating that they are separate from other members of Saxifragaceae *s. l.* According to Hideux & Ferguson (1976), *Vahlia* and *Parnassia* are also similar in many pollen characters. The chromosome numbers of *Vahlia* ($n$ = 6, 9; Hamel, 1953) are also similar to those of *Parnassia,* which has $x$ = 8 and 9 (Gastony & Soltis, 1977). Sequence evidence, however, indicates that *Vahlia* is distantly related to *Parnassia.* Determination of the relationships of *Vahlia* would benefit greatly from more detailed systematic study. Secondary chemistry investigations might help determine the affinities of *Vahlia*; since most of the other taxa in this asterid group produce iridoids, an evaluation of *Vahlia* for the presence or absence of iridoids would be especially valuable.

Broader phylogenetic analyses of Chase et al. (1993) also indicate that *Vahlia* occupies a position basal to many asterid taxa. This position of *Vahlia* is intriguing in light of the fossil record. Friis & Skarby (1981, 1982) described a highly developed, apparently saxifragaceous flower (*Scandianthus*) from the upper Cretaceous period and proposed that Saxifragaceae *s. l.* may have been well differentiated as early as the lower Cretaceous. As noted by Dahlgren (1983), the *Scandianthus* flower is virtually identical to the flower of *Vahlia,* having an inferior, bicarpellate, unilocular ovary with two pendulous placentae, five sepals and petals of approximately equal length, and two separate stigmas (Friis & Skarby, 1981, 1982). The two genera differ only in that *Vahlia* has five stamens and *Scandianthus* ten. Thus, fossil evidence in conjunction with our sequence data raise the possibility that *Vahlia* could be a relict of the ancestral type of many of these asterid families.

## Summary

Our phylogenetic analysis of *rbc*L sequences indicates that, among angiosperm families, Saxifragaceae *s. l.* may represent the most extreme example of a polyphyletic assemblage. These analyses suggest that these taxa represent at least 10 separate evolutionary lines. Furthermore, these separate lineages are distributed among most traditionally recognized subclasses of the dicots. These results are not wholly unexpected, however. Several genera and subfamilies of Saxifragaceae *s. l.* are poorly understood (e.g., Montinioideae, Vahlioideae, Lepuropetaloideae, Phyllonomoideae, Pterostemonoideae, Escallonioideae, Tetracarpaeoideae, Francooideae), and their affinities have actually been much in doubt. In addition, although members of Saxifragaceae *s. l.* are allied with at least 10 separate lineages in our results, the relationships supported by *rbc*L sequence data are in many instances corroborated by other lines of evidence. Numerous different types of data are congruent with *rbc*L-supported alliances in specific instances, but some lines of evidence (such as those derived from embryology, iridoid chemistry, serology, and floral anatomy) are especially notable for the frequency with which they agree with *rbc*L sequence results.

Our *rbc*L sequence data suggest that Saxifragaceae should be composed of only the genera included in the subfamily Saxifragoideae of Schulze-Menz (1964). Data from several sources, including intron loss in the chloroplast gene *rpl*2, restriction site analysis of chloroplast DNA, and morphology all serve to distinguish this group of genera from traditionally allied taxa of Saxifragaceae *s. l.* It seems most appropriate, therefore, to define Saxifragaceae sensu stricto (Saxifragaceae *s. s.*) as consisting only of the approximately 30 genera of subfamily Saxifragoideae, a circumscription of the family that is identical to that proposed by Takhtajan (1987) and Thorne (1992).

Sequence evidence indicates that Iteoideae, Pterostemonoideae, Ribesoideae, Tetracarpaeoideae, Penthoroideae, *Myriophyllum* (Haloragaceae), and Crassulaceae are possible close relatives of Saxifragaceae *s. s.* (Figs. 2, 3). Although sequence data provide little direct support for a monophyletic

alliance composed of these taxa, they do share several features. As reported by Bensel & Palser (1975a, b, c, d) most of these taxa are very much alike in the anatomy and morphology of their flowers. Furthermore, all of these taxa that have been studied have bitegmic crassinucellate ovules and cellular (sometimes helobial) endosperm formation. This combination of features is relatively uncommon in non-magnoliid dicots, the more common combination being bitegmic crassinucellate ovules with nuclear endosperm formation (Dahlgren, 1975b; Philipson, 1974, 1977; Table 2). Serological evidence (Grund & Jensen, 1981) also supports close relationships among many of the same taxa (Saxifragaceae *s. s.*, Crassulaceae, *Ribes*, *Penthorum*). A phylogenetic analysis of many anatomical, morphological, and chemical characters (Hufford, 1992) similarly suggests that Saxifragaceae *s. s.*, Crassulaceae, *Penthorum*, and *Tetracarpaea* are closely related.

An intriguing result of this investigation is the placement of four genera near Saxifragaceae *s. s.* that are usually included in the subclass Hamamelidae: *Cercidiphyllum*, *Daphniphyllum*, *Rhodoleia*, and *Hamamelis* (Figs. 2, 3). These genera have been described as part of the "lower Hamamelidae" (Ehrendorfer, 1989) and, although rarely mentioned as close relatives of Saxifragaceae, they have occasionally been linked with the family (Dickison, 1989). Thorne (1992) included these hamamelid taxa in his Rosanae along with Saxifragales, Rosales, and Cunoniales, as well as the "higher hamamelid" taxa Fagales and Juglandales. Dahlgren (1983) placed Saxifragaceae and many hamamelids in his Rosiflorae, considering Saxifragaceae to be connected to the hamamelid taxa through Cunoniaceae. Grund & Jensen (1981) found a high level of serological affinity between *Hamamelis* and several genera of Saxifragaceae *s. s.* Significantly, this serological affinity is as high as that observed between *Ribes* and Saxifragaceae *s. s.* or between Crassulaceae and Saxifragaceae *s. s.*

In addition to suggesting a narrow definition of Saxifragaceae and indicating several possible relatives, *rbc*L sequence data also indicate that other families often associated with Saxifragaceae *s. s.* (e.g., Cunoniaceae, Greyiaceae, Droseraceae, Cephalotaceae, Gunneraceae, Rosaceae) are not closely related to it. Although Dahlgren (1983), Takhtajan (1987), and Thorne (1992) considered Cunoniaceae to be distantly related to Saxifragaceae *s. s.*, Cronquist (1981) and Schulze-Menz (1964) placed Cunoniaceae in the same order as Saxifragaceae *s. s.* Our *rbc*L sequence evidence is in close agreement with Dahlgren (1983), Takhtajan (1987), and Thorne (1992) in suggesting a distant relationship between Saxifragaceae *s. s.* and Cunoniaceae; only Baueroideae appear close to Cunoniaceae (Figs. 2, 4).

The *rbc*L sequence data also indicate that Greyiaceae are distantly related to Saxifragaceae *s. s.* (Figs. 2, 4). This family is included in the same order or suborder as Saxifragaceae *s. s.* by almost all authors. According to *rbc*L sequence evidence, however, Greyiaceae are allied only with the herbaceous subfamily Francooideae (Figs. 2, 4), an alliance that has several lines of corroborating evidence (see discussion of *Francoa* above).

Results from analysis of *rbc*L sequences also do not indicate a close relationship between Saxifragaceae *s. s.* and Droseraceae (Fig. 1), a family allied closely with Saxifragaceae *s. s.* and other herbaceous subfamilies of Saxifragaceae *s. l.* by Dahlgren (1983), Takhtajan (1987), and Thorne (1992). *Drosera* is, according to sequence evidence, distantly related not only to Saxifragaceae *s. s.* but also to all other subfamilies of Saxifragaceae *s. l.* (Fig. 1). The position of Droseraceae based on sequence evidence (near *Nepenthes*) agrees more closely with the classifications of Cronquist (1981) and Schulze-Menz (1964). On the basis of floral morphology, Cephalotaceae, another insectivorous family, are often thought to be closely related to both Saxifragaceae *s. s.* and Crassulaceae (Nicholls et al., 1985). Sequence data of *rbc*L, however, indicate that Cephalotaceae are most closely allied not with Saxifragaceae *s. s.* or Crassulaceae but with *Platytheca* (Tremandraceae) and Cunoniaceae (Figs. 2, 4).

*Gunnera* is, according to *rbc*L sequence data, also distantly related to Saxifragaceae *s. s.* *Gunnera* has sometimes been included in Haloragaceae (Cronquist, 1981) but has often been treated as the family Gunneraceae and placed close to Saxifragaceae (Dahlgren, 1983; Takhtajan, 1987). The affinities of *Gunnera* have remained uncertain because of an unusual combination of characteristics (e.g., wind pollination, symbiotic algae, unisexual flowers, a bicarpellate unilocular ovary, solitary ovule). The basal position of *Gunnera* in the results of our analysis (Fig. 1) still make identification of its closest relatives difficult, but sequence data obviously do not indicate a relationship with Saxifragaceae *s. s.* or other subfamilies of Saxifragaceae *s. l.*

Rosaceae have been closely associated with Saxifragaceae by Dahlgren (1983) and Cronquist

(1981). Our results, however, suggest that Rosaceae are not closely related to Saxifragaceae *s. s.* but are allied with Ulmaceae, Moraceae, and Rhamnaceae (Figs. 2, 4).

The results of *rbc*L sequence analysis indicate that five subfamilies of Saxifragaceae *s. l.* (Baueroideae, Francooideae, Brexioideae, Parnassioideae, and Lepuropetaloideae) are well separated from Saxifragaceae *s. s.* and associated taxa but are still included within an alliance composed primarily of families usually placed in Rosidae (Figs. 2, 4). Baueroideae and Francooideae are, according to *rbc*L sequence evidence, both allied with families (Cunoniaceae and Greyiaceae, respectively) that have identical embryological characteristics. Brexioideae and Parnassioideae are alike in having a relatively uncommon combination of embryological characteristics: bitegmic tenuinucellate ovules with nuclear endosperm formation, features that otherwise are commonly found only in Ebenales, Primulales, and Theales (Davis, 1966; Philipson, 1974, 1977). The sequence evidence delineates a well-supported alliance that includes Brexioideae and Parnassioideae with the embryologically identical *Euonymus* (Celastraceae). These three taxa also have many similarities in floral anatomy and morphology. Although Lepuropetaloideae are poorly known embryologically, their inclusion in this alliance is well supported by many floral similarities with Parnassioideae.

Another significant result of this study is the finding that five subfamilies of Saxifragaceae *s. l.* (Hydrangeoideae, Escallonioideae, Phyllonomoideae, Montinioideae, and Vahlioideae) are, according to *rbc*L evidence, distantly related to all other subfamilies of Saxifragaceae *s. l.* (Figs. 1, 5). Sequence data suggest instead a placement of these taxa in an expanded asterid alliance (see also Olmstead et al., 1993). Other lines of evidence support these results; these five subfamilies are placed nearest to taxa that are similar in having such characteristics as iridoids and ovules that are unitegmic and tenuinucellate.

## Conclusions

Phylogenetic analysis of *rbc*L sequence data has greatly improved our understanding of the relationships among the morphologically diverse members of Saxifragaceae sensu lato. These data have: (1) shown that Saxifragaceae sensu lato are an extreme example of a polyphyletic angiosperm family, (2) suggested that Saxifragaceae be narrowly defined to consist only of approximately 30 herbaceous genera, (3) indicated possible close relatives of Saxifragaceae sensu stricto, (4) revealed that many traditional relatives of Saxifragaceae sensu stricto are only distantly related, (5) shown that some lines of evidence, especially embryology, iridoid chemistry, and serology, are frequently in close agreement with *rbc*L sequence data, and (6) identified areas in which additional data from molecular as well as more traditional investigations should increase our understanding of angiosperm systematics.

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# PHYLOGENETIC RELATIONSHIPS OF THE GERANIACEAE AND GERANIALES FROM *rbc*L SEQUENCE COMPARISONS[1]

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ABSTRACT

Parsimony analyses of DNA sequence data from the chloroplast *rbc*L gene were used to assess the circumscription and phylogenetic position of the Geraniaceae, generic relationships within the family, and the affinities of the families previously assigned to the order Geraniales. The other families placed in the Geraniales in recent higher-order classifications fall into four well separated lineages, none of which appears to be closely related to the Geraniaceae. Only *Hypseocharis*, often included in the Oxalidaceae, receives strong support as a close relative to the monophyletic Geraniaceae sens. str., as suggested by Boesewinkel on the basis of seed anatomy. Sequence comparisons of *rbc*L provide the first highly resolved phylogeny of the Geraniaceae, indicating that *Pelargonium* is a sister group to the remainder of the family, that *Erodium* and *Geranium* are probable sister genera, and that *Monsonia* and *Sarcocaulon* are either sister genera or are congeneric.

The Geraniaceae sens. str., comprising the five genera *Erodium*, *Geranium*, *Monsonia*, *Sarcocaulon*, and *Pelargonium*, are of particular evolutionary interest in that they exhibit the greatest amount of variation in size and structure of the chloroplast genome known for any family of photosynthetic flowering plants. Substantial increase in the size of the inverted repeat region in at least some taxa of *Pelargonium* is exemplified by the largest known angiosperm chloroplast genome (217 kb in the cultivated geranium, *P.* ×*hortorum*), whereas the loss of one copy of the inverted repeat has resulted in an unusually small chloroplast genome of ca. 120 kb in *Erodium* and *Sarcocaulon* (Palmer et al., 1987; Price et al., 1990). Other unusual features seen in the family include multiple inversions, losses of highly conserved introns, and particularly rapid rates of sequence change in some chloroplast genes (Downie & Palmer, 1992; Downie et al., 1991; Calie et al., unpublished data).

To examine these and other interesting features of the Geraniaceae in an evolutionary context, it is necessary to obtain an independent assessment of the phylogenetic relationships of the family and its close relatives. It has proved difficult to assess generic relationships in the family using morphological or cytological characters because of the paucity of informative characters and the considerable variability within genera (see discussions in Vorster, 1990). Thus we have used sequence comparisons of the chloroplast gene *rbc*L, which has come into wide use in systematic studies of the flowering plants (see discussions in Olmstead et al., 1992; Chase et al., 1993), to attempt to elucidate phylogenetic relationships within the Geraniaceae and to determine which taxa are the most appropriate outgroups for comparison to the family.

Whereas a general consensus exists that the five genera of the Geraniaceae sens. str. are closely related, there has been considerable disagreement as to whether to include several segregate families in the Geraniaceae. The monogeneric Eurasian family Biebersteiniaceae, the monotypic family Dirachmaceae (endemic to the island of Socotra), and the small South American families Ledocarpaceae, Rhynchothecaceae, and Vivianiaceae have been included in the Geraniaceae sens. lat. by Cronquist (1981, 1988) and Thorne (1992), following the classical treatment of Knuth (1912), but excluded from the family by Dahlgren (1989), Robertson

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(1972), Takhtajan (1987), and van der Walt & Vorster (1988). Each of these segregate families differs from the Geraniaceae sens. str. by lacking one or several of its diagnostic combination of gynoecial and fruit characters (an ovary consisting of five two-ovulate locules united to an elongated stylar column, developing into a schizocarpic fruit of five one-seeded units separating from the persistent column; see Robertson, 1972) but needs to be considered as a potential close relative of the Geraniaceae. In addition, Boesewinkel (1988) has provided evidence from seed anatomy that *Hypseocharis*, an Andean genus often placed in the Oxalidaceae, may in fact be the closest relative of the Geraniaceae sens. str., and Thorne (1992) has included this genus in his subfamily Geranioideae.

Families included in the order Geraniales in the recent higher-order classifications of Cronquist (1981, 1988), Dahlgren (1989), Takhtajan (1987), and Thorne (1992) are compared in Table 1. Each of these classifications includes within the order the segregate families noted above, and all except Dahlgren (1989) include the Oxalidaceae and its segregate families Hypseocharitaceae and Lepidobotryaceae. Cronquist (1981, 1988) and Thorne (1992) also included the Balsaminaceae and the glucosinolate-producing families Limnanthaceae and Tropaeolaceae in the Geraniales, whereas Dahlgren (1989) placed the latter two families near the other glucosinolate taxa. Dahlgren (1989) also included the Zygophyllaceae and several small families segregated from it (Balanitaceae, Nitrariaceae, and Peganaceae) within the Geraniales, whereas these taxa have been otherwise assigned to the Sapindales (Cronquist, 1988), Rutales (Takhtajan, 1987), or Linales (Thorne, 1992). Older classifications by the same authors circumscribed the Geraniales still more broadly, e.g., Dahlgren (1980) and Takhtajan (1980) also included the Linaceae and the putatively closely related Erythroxylaceae and Humiriaceae in the order, and Thorne (1983) included the Malphigiaceae and putative relatives as well. As one might expect from the diversity of classifications discussed here, comparison of diagnostic features of the various families purported to be closely related to the Geraniaceae does not indicate strong support from unusual shared derived features of morphology or secondary product chemistry for any of the circumscriptions of the order (see Cronquist, 1981). The main features linking the families of Geraniales in the system of Cronquist appear to be a tendency to have 10–15 stamens and 5-parted gynoecia, neither of which is unique to the group. We have thus attempted to evaluate the relationships of these families by comparison of *rbc*L sequences from a number of different lineages of the subclasses Rosidae and Dilleniidae.

## Materials and Methods

Forty-eight taxa utilized in this study for *rbc*L sequence comparisons and their sources are listed in Table 2. Total genomic DNA was extracted from 1–3 grams of fresh leaf material or an equivalent fresh weight of silica gel-dried leaves using the modified CTAB procedure of Doyle & Doyle (1987). Leaves resistant to grinding (e.g., *Pelargonium* species) were first frozen in liquid nitrogen and then ground prior to extraction. All DNA samples were further purified and concentrated by CsCl-ethidium bromide gradient centrifugation. The complete *rbc*L gene was amplified via the polymerase chain reaction (PCR) using a 5′ primer consisting of the first 26 bases of the gene and a 3′ primer based on a 24-base portion of a stem-loop region ca. 100 bases beyond the gene (Olmstead et al., 1992).

Five taxa in the study (*Geranium grandiflorum*, *Limnanthes douglasii*, *Monsonia emarginata*, *Oxalis dillenii*, *Tropaeolum majus*) were initially sequenced from DNA cloned from PCR products using the strategy of Olmstead et al. (1992) and then rechecked by direct sequencing of double-stranded PCR products, which was used for all other taxa. DNA from PCR was purified by centrifugation in Centricon 100 filters (Amicon) for use in direct sequencing. Double-stranded DNA samples were denatured in a 95°C heat block and plunged immediately into an ice-water slurry to prevent renaturation. Sequencing was performed using the dideoxy chain termination method, utilizing primers supplied by G. Zurawksi. Six forward and six reverse primers were used for each species, and approximately 65–80% of the sequence was read from both strands.

A total of 1,402 bp of sequence was used for phylogenetic comparisons; this excluded the area of the 5′ amplification primer and any extensions of the gene beyond the length of 1,428 bp found in most seed plants. Alignment of the sequences was accomplished by comparison of the sequence of *Nicotiana tabacum*. Parsimony analyses were conducted using PAUP version 3.0q (Swofford, 1991) on Macintosh computers. To identify minimum length trees we used either the heuristic search and MULPARS options with 50 replicate random orders of taxon entry, TBR branch swapping, and steepest descent, or, in the case of the smaller analysis of Geraniaceae, the branch and bound algorithm. Bootstrap analyses (Felsenstein, 1985) and decay analyses (Bremer, 1988) were

TABLE 1. Families included in the Geraniales in recent higher-order classifications of Cronquist (1981, 1988), Takhtajan (1987), and Dahlgren (1989). The classification of the order in Thorne (1992) is the same as that of Cronquist except in that the segregate families Biebersteiniaceae, Dirachmaceae, Ledocarpaceae, and Vivianiaceae are treated formally as subfamilies of the Geraniaceae, and *Hypseocharis* is included in the subfamily Geranioideae of the Geraniaceae rather than the Oxalidaceae. The Zygophyllaceae and its segregate families Balanitaceae, Nitrariaceae, and Peganaceae are assigned to the Sapindales by Cronquist, to the Rutales by Takhtajan, and to the Linales by Thorne.

| Cronquist | Takhtajan | Dahlgren |
|---|---|---|
| Geraniaceae | Geraniaceae | Geraniaceae |
| Geraniaceae | Biebersteiniaceae | Biebersteiniaceae |
| Geraniaceae | Dirachmaceae | Dirachmaceae |
| Geraniaceae | Ledocarpaceae | Ledocarpaceae |
| Geraniaceae | Rhynchothecaceae | Ledocarpaceae |
| Geraniaceae | Vivianiaceae | Vivianiaceae |
| Oxalidaceae | Oxalidaceae | (in Linales) |
| Oxalidaceae | Hypseocharitaceae | (in Linales) |
| Oxalidaceae | Lepidobotryaceae | (in Linales) |
| Balsaminaceae | (in Balsaminales) | (in Balsaminales) |
| Limnanthaceae | (in Limnanthales) | (in Tropaeolales) |
| Tropaeolaceae | (in Tropaeolales) | (in Tropaeolales) |
| | | Balanitaceae |
| | | Nitrariaceae |
| | | Peganaceae |
| | | Zygophyllaceae |

performed using PAUP 3.0q to examine the degree of support for given branches of the cladograms. The number of additional steps required to shift particular taxa into a monophyletic group with the Geraniaceae was examined using the CONSTRAINTS option of PAUP.

## RESULTS

Sequences of *rbc*L were compared for 48 taxa (Table 2), including nine from published sources, 17 unpublished sequences assembled for the global analyses of Chase et al. (1993, provided by M. Chase, E. Conti, D. Soltis, and J. Nugent), and 22 sequences generated in this study, including 14 from the Geraniaceae sens. str. All sequences generated in this study have been deposited in the GenBank. Two sets of parsimony analyses were conducted, the first focusing on the familial and ordinal relationships of the Geraniaceae and Geraniales, and the second focusing on generic relationships within the Geraniaceae sens. str. For the ordinal level comparisons, 39 taxa were chosen to represent each of the families of the Geraniales sensu Cronquist and a variety of other families from the Rosidae and Dilleniidae. These included several groups (e.g., families of Linales, Sapindales, and Capparales) often considered to be related to the Geraniales and representatives of the families grouping with families of the Geraniales in analyses of the broader data set of *rbc*L sequences assembled by Chase et al. (1993). *Tetracentron* (Tetracentraceae) and *Gunnera* (Gunneraceae) were chosen from the Chase et al. (1993) data set as outgroups from near the base of the rosid–dilleniid lineage. The same ingroup topology was obtained when *Platanus* (Platanaceae) was included as a third outgroup.

Parsimony analysis with equal character weighting yielded a single minimum length tree of 1,609 steps (Fig. 1) with a consistency index (CI) of 0.38 excluding unique substitutions and a retention index (RI) of 0.47. The families included in the Geraniales by Cronquist (1988) are placed in five separate clades on the tree: (1) *Oxalis* and *Averrhoa* (Oxalidaceae) with Eucryphiaceae and Cephalotaceae and then linking to a larger group including the Linaceae, (2) *Tropaeolum* and *Limnanthes* in a mustard-oil containing lineage with *Brassica* and then linking to the Malvales and Sapindales, (3) *Wendtia* (Ledocarpaceae) and *Viviania* (Vivianiaceae) grouping together and then linking to the Greyiaceae and Francoaceae, (4) the Geraniaceae sens. str. grouping with *Hypseocharis*, and (5) *Impatiens* (Balsaminaceae) in a morphologically rather disparate group near the base of the tree with Fouquieriaceae and Polemoniaceae. Support for the placement of the putatively gerani-

TABLE 2. Sources of *rbc*L sequences. Taxa are arranged in the classification of Cronquist (1981) except in the recognition of the segregate families Francoaceae, Iteaceae, Parnassiaceae, Hypseocharitaceae, Ledocarpaceae, and Vivianiaceae following Takhtajan (1987). Sequences generated in this study are marked with an asterisk. All voucher specimens have been deposited at IND, except for *Chase 113* (NCU) and *Peñailillo 91000* and *91003* (CONC).

| Family | Species | Source/voucher |
|---|---|---|
| Asteridae | | |
| Solanales | | |
| Polemoniaceae | *Polemonium reptans* | Olmstead et al. (1992) |
| Dilleniidae | | |
| Capparales | | |
| Brassicaceae | *Brassica juncea* | Nugent & Palmer, unpublished |
| Malvales | | |
| Malvaceae | *Gossypium hirtum* | Gulov et al. (1990) |
| Sterculiaceae | *Theobroma cacao** | *Price s.n.* |
| Violales | | |
| Fouquieriaceae | *Fourquieria splendens* | Olmstead et al. (1992) |
| Violaceae | *Viola sororia* | Olmstead et al. (1992) |
| Hamamelidae | | |
| Trochodendrales | | |
| Tetracentraceae | *Tetracentron* sp. | Chase et al., unpublished |
| Rosidae | | |
| Cornales | | |
| Nyssaceae | *Nyssa* sp. | Soltis et al., unpublished |
| Geraniales | | |
| Balsaminaceae | *Impatiens biflora* | Chase et al., unpublished |
| Geraniaceae | *Erodium texanum** | *Van Devender s.n.* |
| | *E. ×variabile** | *Price s.n.* |
| | *Geranium cinereum** | *Price s.n.* |
| | *G. grandiflorum** | *Price s.n.* |
| | *G. macrorrhizum** | *Price s.n.* |
| | *G. maderense** | *Price s.n.* |
| | *G. ocellatum** | *Price s.n.* |
| | *G. palmatum** | *Price s.n.* |
| | *Monsonia emarginata** | *Price s.n.* |
| | *Pelargonium capitatum** | *Price s.n.* |
| | *P. cotyledonis** | *Price s.n.* |
| | *P. existipulatum** | *Price s.n.* |
| | *P. ×hortorum** | *Price s.n.* |
| | *Sarcocaulon vanderietiae** | *Price s.n.* |
| Hypseocharitaceae | *Hypseocharis* sp.* | *Beck s.n.* |
| Ledocarpaceae | *Wendtia gracilis** | *Peñailillo 91003* |
| Limnanthaceae | *Limnanthes douglasii** | *Price s.n.* |
| Oxalidaceae | *Oxalis dillenii** | *Price s.n.* |
| | *Averrhoa carambola** | *Price s.n.* |
| Tropaeolaceae | *Tropaeolum majus** | *Chase 113* |
| Vivianiaceae | *Viviania marifolia** | *Peñailillo 91000* |
| Haloragales | | |
| Gunneraceae | *Gunnera* sp. | Morgan & Soltis (1993) |
| Linales | | |
| Erythroxylaceae | *Erythroxylum* sp. | Chase et al., unpublished |
| Linaceae | *Reinwardtia indica* | Chase et al., unpublished |
| Myrtales | | |
| Lythraceae | *Lythrum subsessilifolium* | Conti et al. (1993) |
| Onagraceae | *Clarkia xantiana* | Conti et al. (1993) |

TABLE 2. Continued.

| Family | Species | Source/voucher |
|---|---|---|
| Polygalales | | |
| Malpighiaceae | *Thryallis* sp. | Chase et al., unpublished |
| Vochysiaceae | *Qualea* sp. | Chase et al., unpublished |
| Rosales | | |
| Cephalotaceae | *Cephalotus* sp. | Morgan & Soltis (1993) |
| Crossosomataceae | *Crossosoma* sp. | Morgan & Soltis (1993) |
| Eucryphiaceae | *Eucryphia* sp. | Morgan & Soltis (1993) |
| Francoaceae | *Francoa sonchifolia* | Soltis et al. (1990) |
| Greyiaceae | *Greyia* sp. | Morgan & Soltis (1993) |
| Hydrangeaceae | *Carpenteria californica* | Soltis et al. (1990) |
| Iteaceae | *Itea virginica* | Soltis et al. (1990) |
| Parnassiaceae | *Parnassia fimbriata* | Soltis et al. (1990) |
| Saxifragaceae | *Heuchera micrantha* | Soltis et al. (1990) |
| Sapindales | | |
| Aceraceae | *Acer* sp. | Chase et al., unpublished |
| Simaroubaceae | *Ailanthus altissima* | Chase et al., unpublished |

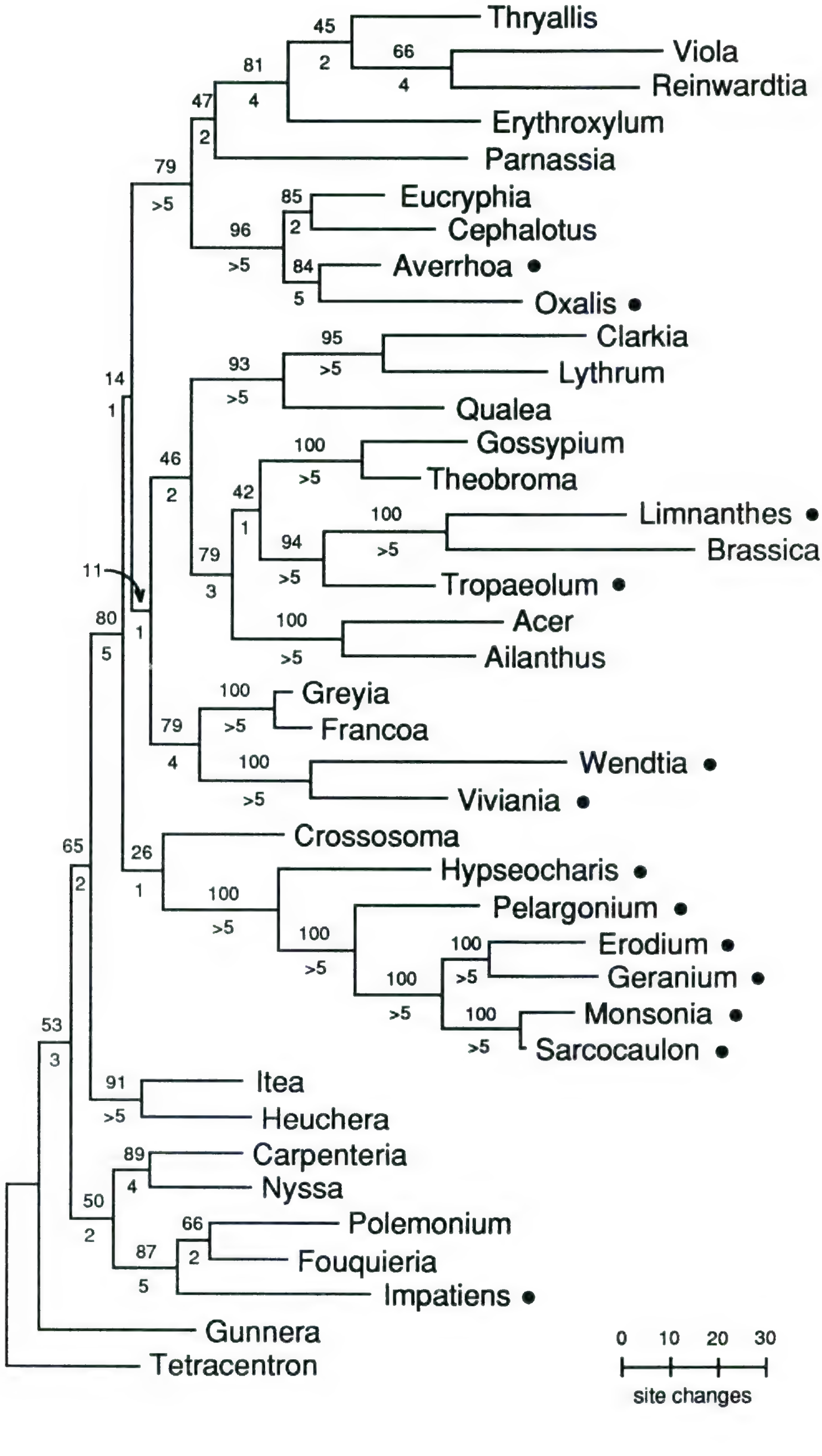
alean taxa in these five groups is relatively strong as indicated by bootstrap values of 79–100% and decay values of four or more steps to collapse the first interior node (Fig. 1).

A series of constraint experiments was used to examine the number of additional steps required to force given taxa into a monophyletic group within the Geraniaceae sens. str. plus *Hypseocharis*. A tree of 74 more steps was needed to obtain a monophyletic group consisting exclusively of taxa from the Geraniales sensu Cronquist. The largest contribution to this increase in length came from forcing the two glucosinolate taxa *Limnanthes* and *Tropaeolum* into the Geraniales, as 36 fewer steps were required when they were no longer included in the constrained group. Conversely, 37 steps beyond the minimum were required to force these two taxa alone into a clade with the Geraniaceae. Twenty steps above the minimum were required to force the two genera of Oxalidaceae into a monophyletic group with the Geraniaceae, while only four steps above the minimum were required to produce a clade of *Viviania*, *Wendtia*, and the Geraniaceae.

The Geraniaceae sens. str. are well supported as a monophyletic group in our analyses, with bootstrap values of 99–100% both in Figure 1 and in additional analyses in which all of our sequences for the family were compared to ten or more outgroup taxa. Outside of *Hypseocharis*, however, which is linked strongly to the Geraniaceae sens. str. by a branch of 25 steps and a bootstrap value of 100%, there is only weak support for the association of any specific taxa with the family. *Crossosoma* (Crossosomataceae) is placed as the next closest outgroup to the family in the minimum length tree, but only one additional step is required to collapse this node, and the associated bootstrap value in this analysis is only 26%. An alternative position for *Crossosoma* at one step more than the minimum is as an isolated taxon forming the first node interior to *Heuchera* and *Itea* near the base of the rosid–dilleniid group.

Based upon the results of the preceding higher-level analysis, a more detailed analysis was undertaken to examine generic relationships in the Geraniaceae using *Hypseocharis* as the outgroup. A single minimum length tree of 330 steps with a CI of 0.68 excluding unique substitutions and an RI of 0.79 was obtained from parsimony with equal weighting (Fig. 2). As in the broader analysis, *Pelargonium* forms a sister group to the remainder of the family. Three of the genera of the family (*Pelargonium*, *Geranium*, and *Erodium*) appear to be monophyletic on the basis of the *rbc*L data, while *Monsonia* and *Sarcocaulon* were represented by only single species in this analysis. *Geranium* and *Erodium* appear as sister genera to one another and then to *Monsonia* plus *Sarcocaulon*. The latter two taxa are supported as a monophyletic group by 100% bootstrap values, in agreement with their close morphological relationship.

With the exception of the closely related species pair *Geranium maderense* and *G. palmatum*, each of the taxa from the large genera *Geranium* and *Pelargonium* included in Figure 2 represents a different section. In *Geranium*, the three sections assigned to subgenus *Robertium* by Yeo (1984),


Thryallis
Viola
Reinwardtia
Erythroxylum
Parnassia
Eucryphia
Cephalotus
Averrhoa
Oxalis
Clarkia
Lythrum
Qualea
Gossypium
Theobroma
Limnanthes
Brassica
Tropaeolum
Acer
Ailanthus
Greyia
Francoa
Wendtia
Viviania
Crossosoma
Hypseocharis
Pelargonium
Erodium
Geranium
Monsonia
Sarcocaulon
Itea
Heuchera
Carpenteria
Nyssa
Polemonium
Fouquieria
Impatiens
Gunnera
Tetracentron
45
2
66
4
81
4
47
2
79
>5
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96
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84
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93
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site changes

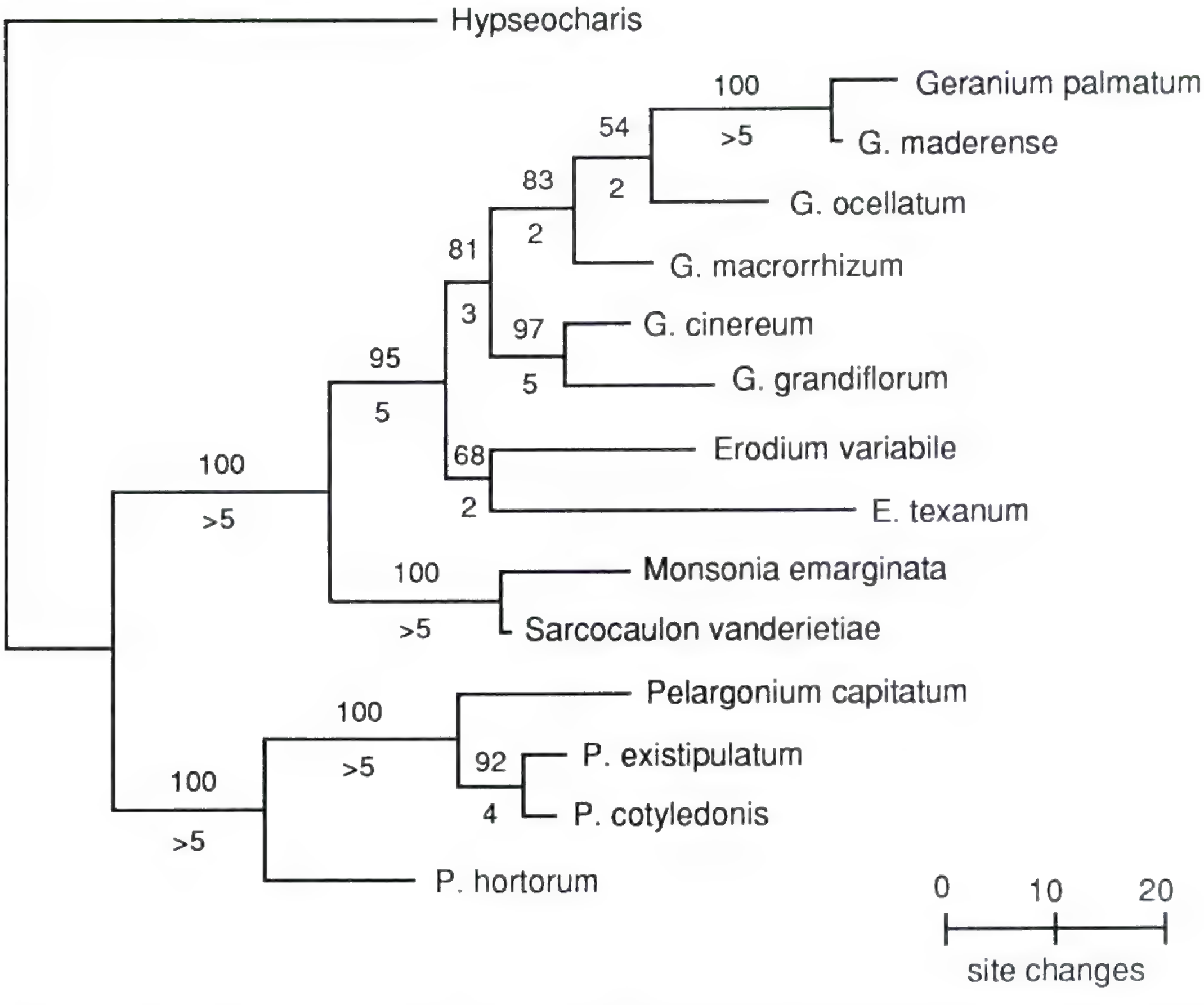


FIGURE 2. The single minimum length Fitch parsimony tree obtained for taxa of Geraniaceae based on comparison of *rbc*L sequences (length = 330 steps, RI = 0.79). Bootstrap values out of 250 replicates are indicated above the branches and decay values are indicated below them.

represented by *G. ocellatum*, *G. maderense* plus *G. palmatum*, and *G. macrorrhizum*, are placed together in a monophyletic group, whereas the individual representatives of subgenus *Geranium* (*G. grandiflorum*) and subgenus *Erodioideae* (*G. cinereum*) group together. The numbers of site changes and associated bootstrap values seen in comparisons within *Erodium*, *Geranium*, and *Pelargonium* are often high and suggest that substantial resolution among other infrageneric groups may be obtained using the *rbc*L gene. One result of particular interest is the unequivocal placement of *Pelargonium cotyledonis*, unusual for the genus in its radially symmetrical flowers and reduced nectar spur, in a position nested within the genus.

## DISCUSSION

### EVALUATION OF SUPPORT FOR BRANCH PATTERNS

In Figures 1 and 2, we compare bootstrap values, decay values, and branch lengths for the various branches of our cladogram. The bootstrap values and decay values are positively correlated, but the correspondence between the two is not monotonic. As an example, the range of bootstrap values corresponding to particular decay values in Figure 1 are as follows: one added step (11–42%, mean = 23%), two added steps (45–85%, mean = 58%), three added steps (53–79%, mean = 66%), four added steps (66–89%, mean = 79%), five added steps (80–87%, mean = 84%), >five

←

FIGURE 1. The single minimum length Fitch parsimony tree obtained from comparison of families of Geraniales and possible relatives using *rbc*L sequence data (length = 1,609 steps, RI = 0.47). Taxa assigned to the Geraniales in the classification of Cronquist (1981) are indicated by dots. Bootstrap values out of 250 replicates are shown above the branches, and decay values (numbers of additional steps needed for a branch to collapse) are given below the branches. The taxa of Geraniaceae included in this analysis are *Erodium* ×*variable*, *Geranium grandiflorum*, *Monsonia emarginata*, *Pelargonium* ×*hortorum*, and *Sarcocaulon vanderietiae*.

added steps (79–100%, mean = 97%). The bootstrap and decay values both appear to provide reasonable indications of which branches on the tree are poorly supported and which are strongly supported, whereas the interpretation of intermediate values is likely to be ambiguous in either case. Displaying both bootstrap and decay values is instructive, since they indicate different aspects of the support for the nodes in the tree and thus tend to reinforce one another. The large amount of computational time required to determine all trees of given lengths more than five steps above the minimum length currently imposes a limit to the precision obtainable with decay analysis. Computational constraints also significantly limit the number of taxa that can be readily evaluated with either decay or bootstrap analysis, leaving only branch lengths and detailed examination of the character distribution to evaluate the support for particular branches when large numbers of taxa are compared. Branch lengths on a given minimum length tree may or may not correspond well to bootstrap values and decay values, presumably depending on the frequency of homoplasy for the characters supporting and internal to a given branch. For example, branch lengths of nine to ten characters in Figure 1 have bootstrap values ranging from 25 to 100% and decay values ranging from one to >five, whereas the bootstrap and decay values correspond much more closely to one another.

## RELATIONSHIPS OF THE GERANIALES

Our results do not provide any substantial support for close relationships of any taxa other than *Hypseocharis* to the Geraniaceae sens. str. The Geraniaceae also group with *Crossosoma* and then with *Greyia*, *Francoa*, and *Viviania* in one of the global analyses of Chase et al. (1993) and in some of the analyses of Morgan & Soltis (1993), but our results would indicate that the character support for the relationships of these groups to the Geraniaceae is weak. While the Geraniaceae are clearly placed in the core group of Rosidae in our analysis (and those of Chase et al., 1993, and Morgan & Soltis, 1993), additional analyses with more of the segregate taxa included and with a larger set of molecular characters will probably be necessary to assess rigorously the precise position of the family within the subclass.

The placement of *Limnanthes* and *Tropaeolum* in a clade of glucosinolate-producing taxa is a consistent feature of *rbc*L sequence comparisons (see particularly Rodman et al., 1993, which includes almost all of the glucosinolate families). Most recent higher-order classifications have placed the Limnanthaceae and Tropaeolaceae in the Geraniales or adjacent orders (see Table 1). However, the occurrence of erucic acid (a compound characteristic of the core capparalean group of glucosinolate taxa) in the Limnanthaceae and Tropaeolaceae seems suggestive of a close relationship between these families and the other glucosinolate taxa, as suggested by Dahlgren (1975). A cladistic analysis of morphological characters by Rodman (1991) placed the Tropaeolaceae within the glucosinolate lineage in a position similar to its placement in the *rbc*L sequence comparisons of Rodman et al. (1993), whereas the morphological trees placed the Limnanthaceae between the Geraniaceae plus Oxalidaceae and the glucosinolate taxa in association with Balsaminaceae. Link (1992) has compared the Limnanthaceae to the Geraniales for a series of floral and embryological characters and concluded that there was no strong evidence favoring a close relationship between them. Thus, because of the high degree of internal consistency of the *rbc*L data (as indicated by the bootstrap values of 94% and 100% in Fig. 1) we favor the inclusion of the Limnanthaceae and Tropaeolaceae within the clade of glucosinolate taxa.

The apparently arbitrary nature of the delimitation of the subclasses Dilleniidae and Rosidae is emphasized by the placement of the Tropaeolaceae and Limnanthaceae (from Cronquist's Rosidae) in a group of glucosinolate taxa largely assigned to the Dilleniidae. As noted by Olmstead et al. (1992) and Chase et al. (1993), the Dilleniidae appear to be a polyphyletic group arising from several separate lineages of Rosidae. As shown in Figure 1, and also Chase et al. (1993) and Rodman et al. (1993), the closest relatives of the glucosinolate lineage appear to be the Malvales (usually assigned to the Dilleniidae) and the Sapindales (usually assigned to the Rosidae).

The position of *Impatiens* (Balsaminaceae) outside of the main lineage of Rosidae and far removed from any other putative groups of Geraniales is unexpected, but appears to be robust to the choice of outgroup and ingroup taxa in the analysis. In the broader *rbc*L analysis of Chase et al. (1993) the Balsaminaceae are placed in a group of rather disparate taxa primarily composed of Ericaceae and other families from the Dilleniidae of Cronquist, but also including the Polemoniaceae (generally assigned to the Asteridae). As discussed by Cronquist (1981), the morphological evidence linking the Balsaminaceae to the Geraniales is weak. The Balsaminaceae differ from the Geraniaceae in embryological features, having tenuinucellate ovules

and cellular endosperm (which are, however, found in the Ericales) rather than crassinucellate ovules and nuclear endosperm.

The separation of the Oxalidaceae from the Geraniaceae in the *rbc*L analysis is contrary to the results of the cladistic analysis of Rodman (1991) and to the recent higher-order classifications of Cronquist (1988), Takhtajan (1987), and Thorne (1992). Our results are in better accord with the groupings of Dahlgren (1989), who placed the Oxalidaceae in the order Linales. The support for the exclusion of the Oxalidaceae from the Geraniales in the *rbc*L analysis is strong, since 20 additional steps are required to force the two families into an adjacent position on the tree, whereas the morphological evidence linking the two families is relatively weak. The two families are similar in generally having 10 to 15 stamens with basally connate filaments, but differ in that the Oxalidaceae have separate styles, abundant endosperm, tenuinucellate ovules, and capsular fruits, whereas the Geraniaceae have fused styles, scant or absent endosperm, crassinucellate ovules, and a specialized type of schizocarpous fruits (see Cronquist, 1981). Boesewinkel (1988) demonstrated that *Hypseocharis*, while often assigned to the Oxalidaceae, has crassinucellate ovules and scant endosperm along with fused styles and is also similar to the Geraniaceae in details of seed wall anatomy not seen in the Oxalidaceae. *Hypseocharis* is also much more similar to the Geraniaceae than the Oxalidaceae in its floral vasculature and has a staminal arrangement similar to that of *Monsonia* and *Sarcocaulon* (Rama Devi, 1991). Thus, *Hypseocharis* appears to be most similar to the Geraniaceae sens. str. in morphology, in exact agreement with the results of our analysis, rather than being intermediate between Oxalidaceae and Geraniaceae. The features shared by *Hypseocharis* and Oxalidaceae (e.g., capsular fruits and the absence of a stylar column) can readily be explained as shared primitive features found in a wide range of rosid taxa. Our results are consistent with the traditional placement of the woody genus *Averrhoa* (the cultivated starfruit) along with *Oxalis* in the Oxalidaceae. The longer branch length leading to *Oxalis* on the cladogram in Figure 1 (44 vs. 13 steps) is striking and would seem to imply a faster rate of sequence change in the shorter-lived herbaceous genus.

Our results provide support for the exclusion of the segregate families Ledocarpaceae and Vivianiaceae from the Geraniaceae, since they are linked robustly to Greyiaceae and Francoaceae instead. Study of additional members of Vivianiaceae and Ledocarpaceae will be necessary before evaluating whether both of these families and the other South American segregate family Rhynchothecaceae should be treated as three separate families. Preliminary data from seed anatomy reported by Boesewinkel (1988) indicate that *Viviania* and also *Dirachma* (Dirachmaceae) are not similar to *Hypseocharis* and the Geraniaceae sens. str. Airy Shaw (1966) earlier suggested that the Socotran genus *Dirachma* is related to the South African family Greyiaceae, presumably on the basis of similar fruit morphology.

In contrast, *Biebersteinia* (the sole genus of the Eurasian family Biebersteiniaceae) appears to be relatively similar to the Geraniaceae in both seed and fruit morphology (Boesewinkel, 1988) and is clearly in need of further evaluation from both morphological and molecular standpoints to assess its relationship to the Geraniaceae. Our results, taken together with those of Boesewinkel, suggest that *Hypseocharis* may appropriately be included in the Geraniaceae as a monogeneric subfamily, while *Biebersteinia* could represent a third subfamily. Further sampling will be needed to assess rigorously the delimitation of the Geraniaceae and Geraniales, but a conservative approach would be to include only *Hypseocharis*, *Biebersteinia*, and the Geraniaceae sens. str. within the order.

### RELATIONSHIPS WITHIN THE GERANIACEAE

Our results agree with morphological data in indicating that the Geraniaceae sens. str. is a well defined monophyletic group. The group is also supported as monophyletic by the loss of the intron in the plastid gene *rpl*16 (Downie & Palmer, 1992), a character that has not yet been examined in *Hypseocharis*. Within the family, our study provides the first available phylogenetic framework. Only the close relationship between *Monsonia* and *Sarcocaulon* has been strongly supported by morphological data. These genera have extremely similar flowers that differ from the rest of the Geraniaceae sens. str. (but resemble *Hypseocharis*) in having 15 stamens rather than 10 or fewer. *Monsonia* and *Sarcocaulon* also share the loss of the highly conserved *rpl*2 intron, otherwise seen throughout the family (Downie et al., 1991). These two genera may appropriately be treated as congeneric, since they differ primarily in that *Sarcocaulon* is a stem succulent and generally has spinescent persistent leaf bases, whereas *Monsonia* is neither succulent nor spiny. Our results do not agree with the suggestion of Rama Devi (1991), on the basis of similarity in staminal arrangement and vasculature, that *Monsonia* and *Sarcocaulon*

are more closely related to *Hypseocharis* than to other genera of Geraniaceae.

The basal split between *Pelargonium* and the rest of the Geraniaceae sens. str., which is well supported in our analyses, has not been predicted based on morphology but is consistent with the much greater level of morphological diversification within *Pelargonium* than in the rest of the family. *Pelargonium* is distinct from the rest of the family in having a nectar spur at the base of the flower (a derived character based on outgroup comparison to *Hypseocharis*) and generally has bilaterally rather than radially symmetrical flowers (a derived feature otherwise observed only in some members of the genus *Erodium*). One of the two species of *Pelargonium* with radially symmetrical flowers (*P. cotyledonis*) appears to be nested within the genus on the basis of our *rbc*L comparisons, suggesting that radial symmetry here represents a reversal from bilateral symmetry. The substantial number of base substitutions observed among representatives of four of the sections of *Pelargonium* augurs well for efforts to use sequence information from the *rbc*L gene to examine relationships among the 14 currently recognized sections of the genus (see van der Walt & Vorster, 1988; Albers et al., 1992) and to assign to section those species of uncertain affinity. Comparisons of the gene among species from the majority of the sections are currently in progress.

The sister-group relationship between *Geranium* and *Erodium* indicated by our results is neither strongly supported nor contradicted by information from morphology and cytology (cf. Yeo, 1984). *Geranium* has a relatively unspecialized floral morphology, but exhibits specialized seed-discharge mechanisms in subgenus *Geranium* and subgenus *Robertium*, whereas *Erodium* often exhibits floral zygomorphy but has the unspecialized "*Erodium*-type" of seed discharge (Yeo, 1984). These two genera do have in common a primarily Northern Hemisphere distribution, whereas *Monsonia*, *Sarcocaulon*, and *Pelargonium* have distributions centered in southern Africa (van der Walt & Vorster, 1988; Yeo, 1984).

The phylogenetic framework that we have obtained from *rbc*L comparisons allows us to begin to examine the likely history of structural changes in the chloroplast genome. Our results suggest that there have been separate losses of a copy of the inverted repeat region in the chloroplast genome in *Erodium* and *Sarcocaulon* and probably separate expansions of the inverted repeat in *Geranium* and *Pelargonium* (see Price et al., 1990). Examination of the plastid genome in *Hypseocharis* will be important in indicating the primitive condition in the family, while comparative studies in the other genera may indicate features of the genome that are associated with these structural changes.

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# TRIBAL RELATIONSHIPS IN ONAGRACEAE: IMPLICATIONS FROM *rbc*L SEQUENCE DATA[1]

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ABSTRACT

The evolutionary relationships among the seven tribes of Onagraceae, the most intensively studied family of intermediate size, have been examined from morphological and molecular perspectives. Previous cladistic analyses of chloroplast (cp) and nuclear ribosomal (nr) DNA restriction sites, nuclear-encoded *rbc*S amino acid sequences, nrRNA nucleotide sequences, and morphological characters, produced trees that agree in defining the tribe Jussiaeeae as the sister group to the rest of the family. However, the relationships among the rest of the tribes are not completely resolved by these analyses. Cladistic analyses of sequence data from the chloroplast encoded *rbc*L gene produced results that bear on two major issues: (i) intertribal relationships within Onagraceae, and (ii) congruence with other cladistic analyses. Sequences of *rbc*L were obtained from all tribes of Onagraceae and from three families that have been proposed as sister taxa of Onagraceae on the basis of other molecular and morphological evidence (Lythraceae, Punicaceae, Trapaceae). Phylogenetic analysis of *rbc*L sequence data produced a single most parsimonious tree, both Fitch and weighted, that defines three strongly supported monophyletic groups within the family: all tribes except Jussiaeeae; Onagreae and Epilobieae; and, most interestingly, Fuchsieae and Circaeeae. The formation of this last clade corroborates the results of the cpDNA restriction site and of the nrRNA sequence data. The data also indicate an apparent slowdown in the rate of *rbc*L sequence divergence in the woody *Fuchsia* lineage relative to the herbaceous *Circaea* lineage. The placements of monogeneric tribes Lopezieae and Hauyeae are not strongly supported. The topology of the *rbc*L tree basically confirms that of the cpDNA restriction site tree. Among the other cladistic analyses, the nrRNA sequence survey produced the tree closest to the *rbc*L tree, followed in order by the *rbc*S amino acid sequence tree, the nrDNA restriction site tree, and the morphological tree.

The Onagraceae consist of seven tribes, 15 genera, and 652 species; six tribes are monogeneric and one (Onagreae) includes nine genera (Hoch et al., 1993; Table 1). Onagraceae presumably originated in West Gondwanaland (the oldest fossil records are from Brazil and California) and reached their highest degree of diversification in North America (Raven & Axelrod, 1974; Raven, 1988). Raven (1988) pointed out that the pollen of Onagraceae is so distinctive it can be recognized in the fossil record from the Late Cretaceous (73–65 mya).

The inclusion of Onagraceae in Myrtales is not questioned (Johnson & Briggs, 1984), but the family is somewhat isolated in the order. The Onagraceae are set off from other families in the order by their peculiar syndrome of morphological and embryological characters: epigynous flowers (Dahlgren & Thorne, 1984); pollen grains with viscin threads (Patel et al., 1984; Skvarla et al., 1976) and peculiar structure of the pollen wall ("paracrystalline beaded" ektexine; Raven, 1988); 4-nucleate *Oenothera*-type embryo sac formation (Tobe & Raven, 1983); abundance of calcium oxalate raphides in vegetative cells (Carlquist, 1975); and presence of septa dividing the sporogenous tissue in the anthers (Tobe & Raven, 1986). The isolation of the family in Myrtales is emphasized by Thorne (1992), who defined Onagraceae as the sole family in suborder Onagrinae.

The Onagraceae are the most intensively studied family of intermediate size from both systematic

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TABLE 1. The seven tribes and the nine species of Onagraceae employed in this study. Information on voucher specimens is listed in the Appendix at the end of this issue.

| Tribe | Genera | Number of species per genus | Species included in this study |
|---|---|---|---|
| Onagreae | 1. *Gongylocarpus* | 2 | |
| | 2. *Gayophytum* | 9 | |
| | 3. *Xylonagra* | 1 | |
| | 4. *Camissonia* | 61 | |
| | 5. *Calylophus* | 6 | |
| | 6. *Gaura* | 21 | |
| | 7. *Oenothera* | 123 | *O. elata* HBK |
| | 8. *Stenosiphon* | 1 | |
| | 9. *Clarkia* | 44 | *C. xantiana* A. Gray |
| Epilobieae | 10. *Epilobium* | 168 | *E. angustifolium* L. |
| Lopezieae | 11. *Lopezia* | 22 | *L. riesenbachia* Plitman, Raven & Breedlove |
| Fuchsieae | 12. *Fuchsia* | 102 | *F. cyrtandroides* J. Moore |
| Circaeeae | 13. *Circaea* | 7 | *C. alpina* L. |
| Hauyeae | 14. *Hauya* | 2 | *H. elegans* DC. |
| Jussiaeeae | 15. *Ludwigia* | 82 | *L. peruviana* (L.) Hara<br>*L. peploides* (HBK) Raven |

and evolutionary perspectives (Raven, 1988; Sytsma & Smith, 1992). Detailed studies exist for morphology–anatomy (Eyde, 1982, on flowers; van Vliet & Baas, 1984, on xylem); embryology (Tobe & Raven, 1983); palynology (Patel et al., 1984); reproductive biology (Raven, 1979); phytochemistry (Averett & Raven, 1984; Dahlgren & Thorne, 1984); and molecules (Bult & Zimmer, 1993; Crisci et al., 1990; Martin & Dowd, 1986; Sytsma & Smith, 1992; Sytsma et al., 1991b).

The cladistic analyses carried out on such data have produced cladograms based on chloroplast DNA (cpDNA) restriction sites (Sytsma et al., 1991b), nuclear ribosomal RNA (nrRNA) sequences (Bult & Zimmer, 1993), nuclear ribosomal DNA (nrDNA) restriction sites (Crisci et al., 1990), amino acid sequences of the nuclear-encoded small subunit of ribulose bisphosphate carboxylase (*rbc*S; Martin & Dowd, 1986), and morphology (Hoch et al., 1993). These trees are congruent in indicating *Ludwigia* (tribe Jussiaeeae) as the sister group to the rest of the family but show some disagreement in the relationships among the other tribes. *Ludwigia* possesses a number of plesiomorphic features, including the absence of a floral tube beyond the ovary and the presence of up to seven parts in its floral whorls. The relationships among the rest of the tribes are not clear, except that the other four monotypic tribes (Fuchsieae, Circaeeae, Lopezieae, and Hauyeae) exhibit a greater number of plesiomorphic features than do either Epilobieae or Onagreae (nine genera).

The remarkable amount of morphological and molecular information available for the Onagraceae, although often conflicting, will provide the framework for comparisons with sequence data of the plastid-encoded large subunit of ribulose bisphosphate carboxylase (*rbc*L) described in this study. The two goals of this phylogenetic analysis of Onagraceae are: (1) to derive a detailed set of relationships among the tribes of Onagraceae using *rbc*L sequence data; (2) to determine congruence between the *rbc*L cladogram and that obtained from cpDNA restriction site mapping analysis, and subsequently from nrRNA sequence, *rbc*S amino acid sequence, nrDNA restriction site, and morphology data sets. The *rbc*L and cpDNA restriction site mapping data sets for the Onagraceae are mutually inclusive for taxa but completely exclusive for characters (i.e., no restriction enzymes mapped recognize variable sites within *rbc*L).

The applicability of *rbc*L sequence information to resolving relationships within families has seldom been tested (but see Doebley et al., 1990, on Poaceae; Soltis et al., 1990, on Saxifragaceae for studies in which intrafamilial relationships have been examined in part). A separate, detailed analysis is planned to examine the global implications of all data sets for the family (Sytsma et al., in prep.).

## Methods

Twelve species, representative of the seven tribes of Onagraceae and of three myrtalean outgroups, are considered in the present study. Table 1 lists the nine species of Onagraceae employed in this analysis. Two species of *Ludwigia* (*L. peruviana* (L.) Hara of sect. *Myrtocarpus* and *L. peploides* (HBK) Raven of sect. *Oligospermum*), representatives of divergent lines in the genus (Eyde, 1981), were sampled because *Ludwigia* is universally indicated as the sister genus to the rest of the family.

Total DNAs of all but *Oenothera* were extracted according to the method of Smith et al. (1991) from leaves kept at −80°C. For nine of these 12 taxa, excluding *Oenothera*, *Clarkia*, and *Epilobium*, the chloroplast *rbc*L gene was amplified by the polymerase chain reaction (Mullis et al., 1986; Erlich, 1989), using 'AmpliTaq' kits, a Perkin-Elmer Cetus Thermal Cycler, a 5′ primer that anneals to the first 26 base pairs of the gene and a 3′ primer that anneals to a flanking region downstream from the 3′ end. Therefore, for these nine taxa, it was possible to obtain the entire *rbc*L nucleotide sequence with the exclusion of the first (but generally highly conserved) 26 nucleotides.

The DNAs of two of the remaining three species, *Epilobium angustifolium* L. and *Clarkia xantiana* A. Gray, were digested with *EcoR*I (which cuts 10 base pairs internal to the 5′ end and 21 base pairs internal to the 3′ end of the *rbc*L gene) and ligated into pUC19 (later transferred into Bluescript-psk). Plasmids containing the *rbc*L insert (using purified segments of *rbc*L from *Nicotiana* as heterologous probes) were recovered from transformed colonies and purified over cesium chloride gradients. For these two species, the first 10 and the last 21 base pairs are thus missing in the cloned segments. The last 21 missing base pairs were later obtained for *Clarkia xantiana* following PCR amplification of total DNA as described above. The *rbc*L sequence for *Oenothera elata* HBK (ex *O. hookeri*) published by Winter & Herrmann (1988) was utilized. Because this *rbc*L gene was cloned using *EcoR*I, the last 21 base pairs of *Oenothera* are lacking, as with *Epilobium*.

Sequence data were obtained by the Sanger dideoxy method (Sanger et al., 1977) on double-stranded in-vitro amplified products (Gyllensten, 1989) using internal primers (provided by G. Zurawski) and Sequenase 2.0 (United States Biochemical). In most instances, DNA fragments up to 300 nucleotides long were resolved on 6% acrylamyde gels, but 5% Long Ranger gels (AT Biochem) were employed in order to separate DNA fragments up to 500 nucleotides long. These longer fragments were obtained by using a proportion of 1.5 μl extension mix to 1 μl termination mix (both provided in the USB-Sequenase kit) in the termination reactions. The critical step in the method of sequencing directly off the gene-cleaned, double stranded *rbc*L gene involves a heat shock immediately followed by a cold shock (James E. Anderson, pers. comm.). The annealing mixture, formed by the *rbc*L DNA template and the primer, is boiled for three minutes to denature the double stranded DNA, and then plunged into liquid nitrogen. The labeling mixture is then added to the annealing mixture while the latter is thawing in the tube held between fingers. The termination reactions are performed according to the instructions of the USB-Sequenase kit.

Sequences were directly aligned onto a reference sequence template of the *rbc*L sequence of *Nicotiana tabacum* L. and, subsequently, of *Clarkia xantiana*. To ascertain that the 12 sequences obtained belonged to coding genes, the nucleotide sequences were translated to the corresponding amino acid sequences with the TRANSLATE command in the University of Wisconsin-Genetics Computer Group (UW-GCG) package. Missing nucleotide positions are listed in the legend of Table 2.

The phylogenetic analyses were performed using the parsimony algorithms and tree analysis options of the PAUP 3.0r program (Swofford, 1991) on a Macintosh IIsi computer. Only putatively informative characters were included in the analyses; autapomorphic characters were added later to the terminal branches of the resulting most parsimonious phylogram. Various approaches were followed, including Fitch (1971) parsimony (with and without the third codon position), character state-weighting, decay analysis, randomization of trees, and analysis of constrained trees. The ACCTRAN (accelerated transformation optimization) option was employed in all analyses. BRANCH AND BOUND search was used to find the most parsimonious Fitch trees, for bootstrap analysis, decay analyses, and analyses employing character state stepmatrices. Bootstrap analysis (see Felsenstein, 1985, 1988) was performed on the matrix of the potentially informative characters to provide a sense of the support of each clade in the resulting majority rule trees. We are aware of the limitations and possible misuse of the bootstrap procedure (see Sanderson, 1989; Wendel & Albert, 1992), but believe that bootstrap analysis (and decay analysis, see below) can provide useful insight concerning how this data set supports different clades.

The decay analysis was accomplished by saving

TABLE 2. Data matrix of the 86 informative characters resulting from the *rbc*L sequences of the 12 taxa examined. Codon positions other than the third are indicated in the top row (bold face). Nucleotide positions identical to the positions of *Clarkia* are indicated by a dot. Missing nucleotide positions are indicated by "?". Additional noninformative nucleotide positions missing from the entire *rbc*L data set are: *Clarkia*: 705; *Punica*: 391–393, 636–638; *Lythrum*: 1074, 1075, 1282, 1283, 1341, 1342; *Ludwigia peruviana*: 392, 393; *L. peploides*: 392, 393; *Hauya*: 392; *Fuchsia*: 902, 903; *Circaea*: 87; *Lopezia*: 250, 663, 696, 720–725, 1072. Information on the length of the *rbc*L sequences and their GenBank accession numbers is listed in the Appendix at the end of this issue.

| Codon position | 1 21 12 2 11 12 12 11 2 1 21 1 1 1 1 |
|---|---|
| Nucleotide position | 111111111111111111111111111111 |
| | 111222333333444444444445555555666667777778889999990000111111222222222333333334 |
| | 224446822717801346622233556789123466601158457888036235568256712234700134457880233458 0 |
| | 782582441879329205234793409243898434560285213106916173180208016357066926257845205859 98 |
| Taxon | |
| *Clarkia* | AAGCCACAACCAGGTCGTAGCGAGTCTCGGCCGACTGTCACTGCCCGTCTGCATCAGTTTACTTGAAATTTAAGGAACGGATTGAC |
| *Trapa* | ·····C·TGTAC·A·TAA·CA·A·T·ATTTGTG··GGG····T··T··TGC·C··GA·TAC·TG··CAG··TG·AAACCATGG |
| *Punica* | ··A·T···C·T?TA··A···A··AC··T·ATTTG·G··GGG··T····T··TGCT··GG··TGC·T·GCCA···T···AACCATGG |
| *Lythrum* | ··A·T···C·T·TACTA·TAA·CA···T·ATTTGTG··GGG·TTGT··A·CTGCTCA·AAGT·C··GGCCAT··TG·AAACC·AGG |
| *Ludwigia peruviana* | ··ATTG·GC·TGTAC·A·T··T·ACA·T···TT··ATGG·G·T·G··GTC·T·C··A·G····AT·GGCCAT··T·C·A·C···GG |
| *Ludwigia peploides* | ··ATTG·GC·TGTACTACT··T·ACA·T···TT··ATGG·G·T·G··GTC·T·C····G··TAATTGGCCAT··T·C·A·C···GG |
| *Hauya* | ··ATT···C··GTAC·A·T····AC·····TT·TC··A·····T···?··C·?G·GTAC·TGGCCA···T···A···A··· |
| *Fuchsia* | ·G··T···C··GTACTA·T·····TT·TC··A··G··G···T··T····GG·GT··?CGGC·C··AT····· |
| *Circaea* | GG··T··?CG·?TACTA·T·A·····G···T··TC··A··G··G·A·T·CTG····G···TA··CGGC·C·GAT···A··C···· |
| *Lopezia* | G·A·T···CG·GTAC···T····AC·CTA··TT··C··A·····T····C····G·····TGG·CC·G····AA····· |
| *Epilobium* | ··A···T····G·AC··CT···T··T·GAAT·T·····A·····C·····C·····G·CC·····? |
| *Oenothera* | ··A···T····G··C···T·A·····C·····A·A·G·····G·C·····G···? |

all the trees that are *n* steps longer than the shortest tree. The resulting strict consensus trees indicate which clades collapse to an unresolved polytomy at each extra step, thus providing a measure of the robustness of the monophyly of each clade in the minimal tree (see Bremer, 1988; Graham et al., 1991; Mishler et al., 1991; Smith & Sytsma, 1990, for examples).

The stepmatrix described in Albert et al. (1993; see also Albert & Mishler, 1992) was employed for character-state weighting. This stepmatrix takes into consideration known transition versus transversion biases for each position in the codon by assigning different weights to transitions and transversions for each position. In order to reflect lower probability of occurrence, transversions are weighted more than transitions: the highest weight is assigned to transversions in the second codon position, the second highest to transversions in the first codon position, and the lowest to transversions in the third codon position. An additional analysis of the *rbc*L data involved the deletion of all third codon-position changes.

Phylogenetic signal in the *rbc*L data was examined by performing the option RANDOM TREES in PAUP. Hillis (1991) provided critical values for g1 statistics (a common measure of left skewness of a distribution) of tree length distributions for up to eight taxa ($P < 0.05$ and $P < 0.01$). In order to compare the results of *rbc*L trees randomization with the critical values provided by Hillis, the three outgroup taxa (*Punica granatum* L., *Trapa natans* L., *Lythrum hyssopifolia* L.) and one taxon of Onagraceae were eliminated from the 12 taxa included in this *rbc*L study. As the monophyly of Jussiaeeae is not under dispute (see also results below), *Ludwigia peploides*, one of the two taxa representing this tribe, was eliminated from the data set. The frequency distribution of lengths of 10,000 random unrooted trees for the eight taxa left was analyzed.

The topology and lengths of other published trees for Onagraceae using different data sets were investigated by user tree options in PAUP. The choice and number of taxa represented in these alternative trees did not always match those of the present *rbc*L study. Therefore, in cases such as with the nrDNA restriction site tree (Crisci et al., 1990), where Lopezieae is absent, missing taxa were placed as in the *rbc*L tree. In this way the number of extra steps required to force the *rbc*L sequence data onto the topologies generated from the other data sets was minimized.

*Punica granatum* (Punicaceae), *Lythrum hyssopifolia* (Lythraceae sensu stricto) and *Trapa natans* (Trapaceae) were used for global outgroup comparison (Maddison et al., 1984). Based on cladistic analysis of morphological features, Johnson & Briggs (1984) indicated that the sister group to the Onagraceae includes Lythraceae sensu lato and/or Trapaceae, the latter a monotypic family. Lythraceae are characterized by several plesiomorphic features and by a wide range of morphological variation that suggest a central position in the order Myrtales (Dahlgren & Thorne, 1984). Both Johnson & Briggs (1984) and Dahlgren & Thorne (1984) included other small families within Lythraceae, most notably the monogeneric family Punicaceae. *Punica* consists of only two species, *P. granatum*, the pomegranate, and *P. protopunica* Balf. f., which may resemble the wild ancestor of the cultivated pomegranate (Dahlgren & Thorne, 1984). Most authors treat Punicaceae as a separate family, but wood anatomy and other morphological data suggest an inclusion within Lythraceae (Bridgewater & Baas, 1978).

## Results

The 12 *rbc*L sequences analyzed for this study contain 195 variable nucleotide positions; of these, 109 are autapomorphies, leaving 86 informative characters. Among the 195 variable positions, 137 (70.3%) are third codon positions, 34 (17.4%) are first codon positions, and 24 (12.3%) are second codon positions.

The data matrix of the 86 informative characters used in the phylogenetic analysis is shown in Table 2. The last informative character is position 1408, indicating that no variation is found among the last 20 nucleotides of the 10 taxa sequenced to the end of the gene. Therefore, it can be assumed that the only informative character missing for the two cloned genes of *Oenothera elata* and *Epilobium angustifolium* is position 1408.

Of the 86 putatively informative characters, 69 (79.7%) are binary characters, 15 (17.8%) are 3-state characters, and two (2.4%) are 4-state characters. Therefore, the minimum number of character-state changes possible (i.e., no homoplasy present) with this data set is 105. The informative changes are distributed differently, as expected, among the codon positions: 63 (73.2%) third codon-position changes, 16 (18.6%) first codon-position changes, and only seven (8.1%) second codon-position changes. The transition:transversion ratio among all possible changes between

TABLE 3. Matrix of pairwise distances, based on the number of nucleotide differences between taxa. Distances are reported as percentage. Acronyms: CLA = *Clarkia*; TRA = *Trapa*; PUN = *Punica*; LYT = *Lythrum*; PER = *Ludwigia peruviana*; PEP = *L. peploides*; HAU = *Hauya*; FUC = *Fuchsia*; CIR = *Circaea*; LOP = *Lopezia*; EPI = *Epilobium*; OEN = *Oenothera*.

| | CLA | TRA | PUN | LYT | PER | PEP | HAU | FUC | CIR | LOP | EPI | OEN |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CLA | — | 5.7 | 4.4 | 6.0 | 4.1 | 4.4 | 2.9 | 2.6 | 3.8 | 3.2 | 3.4 | 1.9 |
| TRA | | — | 3.9 | 4.4 | 4.8 | 4.7 | 4.1 | 4.8 | 5.6 | 5.2 | 6.4 | 5.8 |
| PUN | | | — | 3.9 | 3.5 | 3.4 | 2.8 | 3.5 | 4.3 | 3.8 | 5.4 | 4.6 |
| LYT | | | | — | 4.4 | 4.6 | 4.4 | 4.6 | 5.3 | 5.3 | 6.7 | 5.7 |
| PER | | — | 0.9 | 2.7 | 3.0 | 4.3 | 3.3 | 4.9 | 3.8 | | | |
| PEP | | | — | 2.5 | 2.9 | 4.1 | 3.5 | 5.2 | 4.2 | | | |
| HAU | | | | — | 1.4 | 2.7 | 2.1 | 4.0 | 3.1 | | | |
| FUC | | | | | — | 1.7 | 2.5 | 4.0 | 2.7 | | | |
| CIR | | | | | | — | 3.4 | 5.1 | 3.7 | | | |
| LOP | | | | | | | — | 4.2 | 3.3 | | | |
| EPI | | | | | | | | — | 3.3 | | | |
| OEN | | | | | | | | | — | | | |

states is 1.51, versus the expected value of 0.5, which implies approximately a three-fold transition bias.

The intertribal pairwise distance, based on overall sequence similarity, between Fuchsieae and Circaeeae is lower (1.7%) than the intergeneric distance between *Clarkia* and *Oenothera* (1.9%) in the tribe Onagreae (Table 3). The highest *rbc*L sequence divergence (5.2%) within the family Onagraceae is found between *Ludwigia peploides* (tribe Jussiaeeae) and *Epilobium angustifolium* (tribe Epilobieae). Including the outgroup taxa, the highest divergence (6.7%) is seen between *Lythrum hyssopifolia* (Lythraceae) and *Epilobium angustifolium* (Onagraceae).

The g1 value of −0.8849 obtained for the distribution of 10,000 random trees is much smaller than the critical value of −0.47 ($P < 0.01$) furnished by Hillis (1991) for eight taxa, thus providing strong evidence that phylogenetic signal is present in the *rbc*L data set. To assess if evolutionary "noise" was introduced by nucleotide changes occurring at the third codon position, the distributions of 10,000 random trees were re-examined by using only third codon-position changes (g1 = −0.8406) and by eliminating all third codon-position changes (g1 = −1.0066). These g1 values indicate that only an insignificant amount of "noise" is introduced by changes at the third codon positions.

The analysis of the informative *rbc*L sites yielded a single most parsimonious Fitch tree (Fig. 1). The tree is 168 steps long, with a Consistency Index (CI) of 0.625 and a Retention Index (RI) of 0.670. The CI value is considerably higher than the CI of about 0.3 expected for 12 taxa in a molecular data set (Sanderson & Donoghue, 1989). The numbers of apomorphies and the bootstrap values supporting each branch are reported on the Fitch tree (= majority rule tree from bootstrap analysis); the number of additional autapomorphies (not included in the original data set; Table 2) are indicated in parentheses for the terminal branches of the tree (Fig. 1). The fundamental features of the tree, such as the numbers of apomorphies supporting each branch, the numbers of consistent (i.e., CI = 1) apomorphies, transitions and transversions, codon positions, bootstrap values and decay order, are summarized in Table 4.

The lowest bootstrap value of the tree (44%) indicates the placement of *Hauya* between the tribe Jussiaeeae and the rest of the family as the weakest branch. This result agrees with the observation that only five changes support this placement of *Hauya* and that only two of these are consistent. The second weakest branch in the tree is the placement of *Lopezia* as the sister group to the clade formed by Epilobieae and Onagreae. This placement of *Lopezia* is supported by a low bootstrap value (56%) and by five changes, only one of which is consistent (one less than *Hauya*). The weak placements of *Hauya* and *Lopezia* are further reflected in the loss of resolution in the consensus tree of trees one step longer (Fig. 2A). The third weakest branch of the tree is that defining the tribe Onagreae (represented by *Clarkia* and *Oenothera*), which is recovered as a monophyletic clade in only 70% of the replications. The Onagreae clade is supported by five changes, of which only one is consistent (see Table 4). The monophyly of the

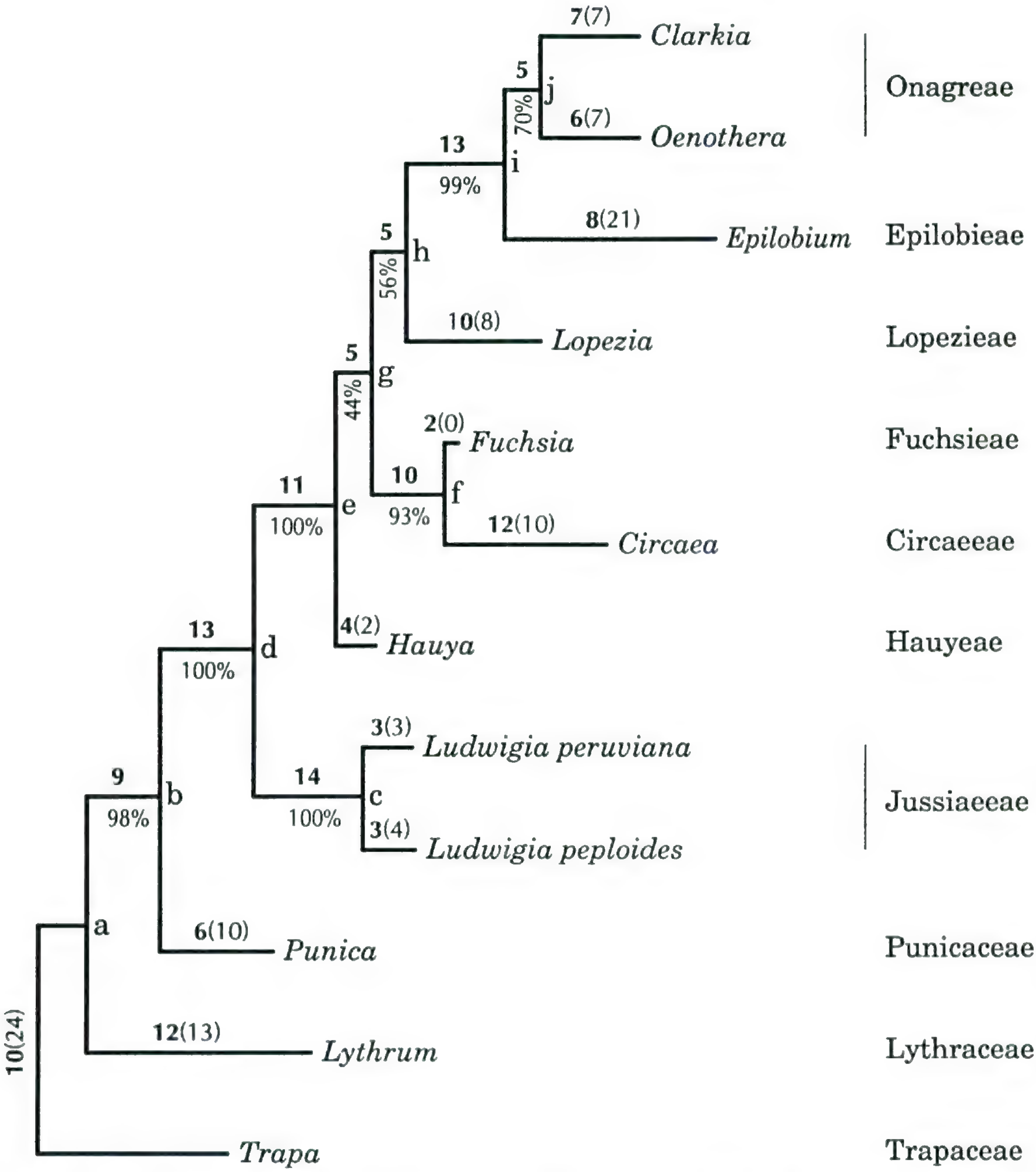


FIGURE 1. The most parsimonious, 168-step tree (represented here as a cladogram with branch lengths) resulting from analysis of *rbc*L sequences of nine taxa of Onagraceae and three outgroup families. *Punica*, *Lythrum*, and *Trapa* are used as simultaneous outgroups. The numbers of apomorphies supporting each clade are indicated in boldface above each branch. The numbers of autapomorphies in the terminal branches are indicated in parentheses. Bootstrap values are reported below the branches. Each node is identified by a small letter. The topology of the weighted tree is identical.

Onagreae is lost in the decay analysis at trees two steps longer (Fig. 2B).

All the remaining clades of the tree are strongly supported by the bootstrap (BS) analysis: (i) all Onagraceae exclusive of *Ludwigia* (BS = 100%); (ii) the two representatives of *Ludwigia* (BS = 100%); (iii) Onagreae–Epilobieae (BS = 99%); (iv) Punicaceae as the sister group to Onagraceae (BS = 98%); (v) *Fuchsia–Circaea* (BS = 93%). These high bootstrap values are correlated with the number of changes supporting these clades (see Fig. 1).

Decay analysis supports the strength of these clades. The monophyly of Onagraceae is lost at

eight (= 4.8%) extra steps (176 steps; 78 trees), when *Lythrum* and *Punica* form a polytomy with Onagraceae (Fig. 2E). Two clades, Onagreae–Epilobieae and Jussiaeeae, survive the breakdown of the familial clade (Fig. 2E). The monophyly of the tribe Jussiaeeae is especially well supported: this clade is lost only at 13 (7.7%) extra steps (Fig. 2G). Of these changes, a large proportion (nine, or 64%) is not affected by homoplasy, and six (42%) are transversions.

The analysis of constrained trees clearly indicates that the topology of the *rbc*L tree is closest to that of the tree based on chloroplast DNA restriction sites; only one extra step is necessary in order to reach the topology of the cpDNA restriction site tree (Fig. 3B). The second closest tree (Fig. 3C: two extra steps) is the nrRNA sequence tree, followed by the *rbc*S amino acid sequence tree (Fig. 3D: eight extra steps), the nrDNA restriction site trees (Fig. 3E: 10 extra steps for the Dollo parsimony, 50% majority rule consensus tree and 12 extra steps for the Wagner parsimony, 50% majority rule consensus tree), and, finally, the morphological tree (Fig. 3F: 14 extra steps).

The application of the character-state stepmatrices simultaneously to the first, second, and third codon position yields the same tree obtained by simple Fitch parsimony (Fig. 1). Elimination of all the changes that occur at the third codon position produces four equally parsimonious trees. In the strict consensus tree (Fig. 4) Onagreae and Onagraceae become paraphyletic groups (respectively, *Oenothera* forms a clade with *Epilobium*, and *Punica* falls within Onagraceae). Additionally, *Lopezia*, *Hauya* and *Punica* collapse to a polytomy with the Jussiaeeae clade and the clade formed by the rest of Onagraceae.

## Discussion

Cladistic analyses of *rbc*L sequence variation, using Fitch or weighted character-state parsimony, provide a single most parsimonious tree (Fig. 1) for Onagraceae and outgroup families. Many of the clades defined in this tree are strongly supported by bootstrap and decay analyses. On the other hand, trees produced by eliminating third codon positions portray evolutionary relationships difficult to support based on other lines of evidence (Fig. 4). This result suggests that changes at the third codon position in *rbc*L, far from producing mere evolutionary noise, are phylogenetically informative within Onagraceae.

The *rbc*L sequence data permit a re-evaluation of evolution within Onagraceae and allow for com-

Table 4. Summary of the major features of the most parsimonious tree in Figure 1. The nodes are indicated by small letters (see tree of Fig. 1). The acronyms are the same used in the legend of Table 3. The number of autapomorphies in the terminal branches (indicated in parentheses in the tree of Fig. 1) is not reported in this table. The numbers reported for the decay order indicate the number of extra steps necessary to collapse a branch to a polytomy. na = not applicable; BS = bootstrap.

| Branch | TRA-a | a-b | b-d | d-e | e-g | g-h | h-i | i-j | j-CLA | j-OEN | i-EPI | h-LOP | g-f | f-FUC | f-CIR | e-HAU | d-c | c-PER | c-PEP | b-PUN | a-LYT |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Apomorphies (all) | 10 | 9 | 13 | 11 | 5 | 5 | 13 | 5 | 7 | 6 | 8 | 10 | 10 | 2 | 12 | 4 | 14 | 3 | 3 | 6 | 12 |
| Transitions | 7 | 5 | 11 | 7 | 4 | 4 | 9 | 4 | 6 | 2 | 5 | 8 | 7 | 2 | 5 | 1 | 3 | 2 | 2 | 2 | 5 |
| Transversions | 3 | 4 | 2 | 4 | 1 | 1 | 4 | 1 | 1 | 4 | 3 | 2 | 3 | 0 | 7 | 3 | 11 | 1 | 1 | 4 | 7 |
| Codon-positions 1 | 1 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 1 | 2 | 0 | 2 | 3 | 1 | 1 | 3 | 4 | 0 | 0 | 2 | 2 |
| 2 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 1 | 1 |
| 3 | 9 | 5 | 12 | 10 | 2 | 5 | 11 | 5 | 5 | 4 | 8 | 6 | 7 | 1 | 9 | 1 | 8 | 3 | 3 | 3 | 9 |
| Apomorphies (CI = 1) | 0 | 6 | 5 | 7 | 2 | 2 | 7 | 1 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 2 |
| Transitions | 0 | 3 | 4 | 3 | 1 | 1 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 |
| Transversions | 0 | 3 | 1 | 4 | 1 | 1 | 3 | 0 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 2 |
| Decay order | na | 6 | 8 | 7 | 1 | 1 | 9 | 2 | na | na | na | na | 7 | na | na | na | 13 | na | na | na | na |
| BS(%): Fitch tree | na | 98 | 100 | 100 | 44 | 56 | 99 | 70 | na | na | na | na | 93 | na | na | na | 100 | na | na | na | na |

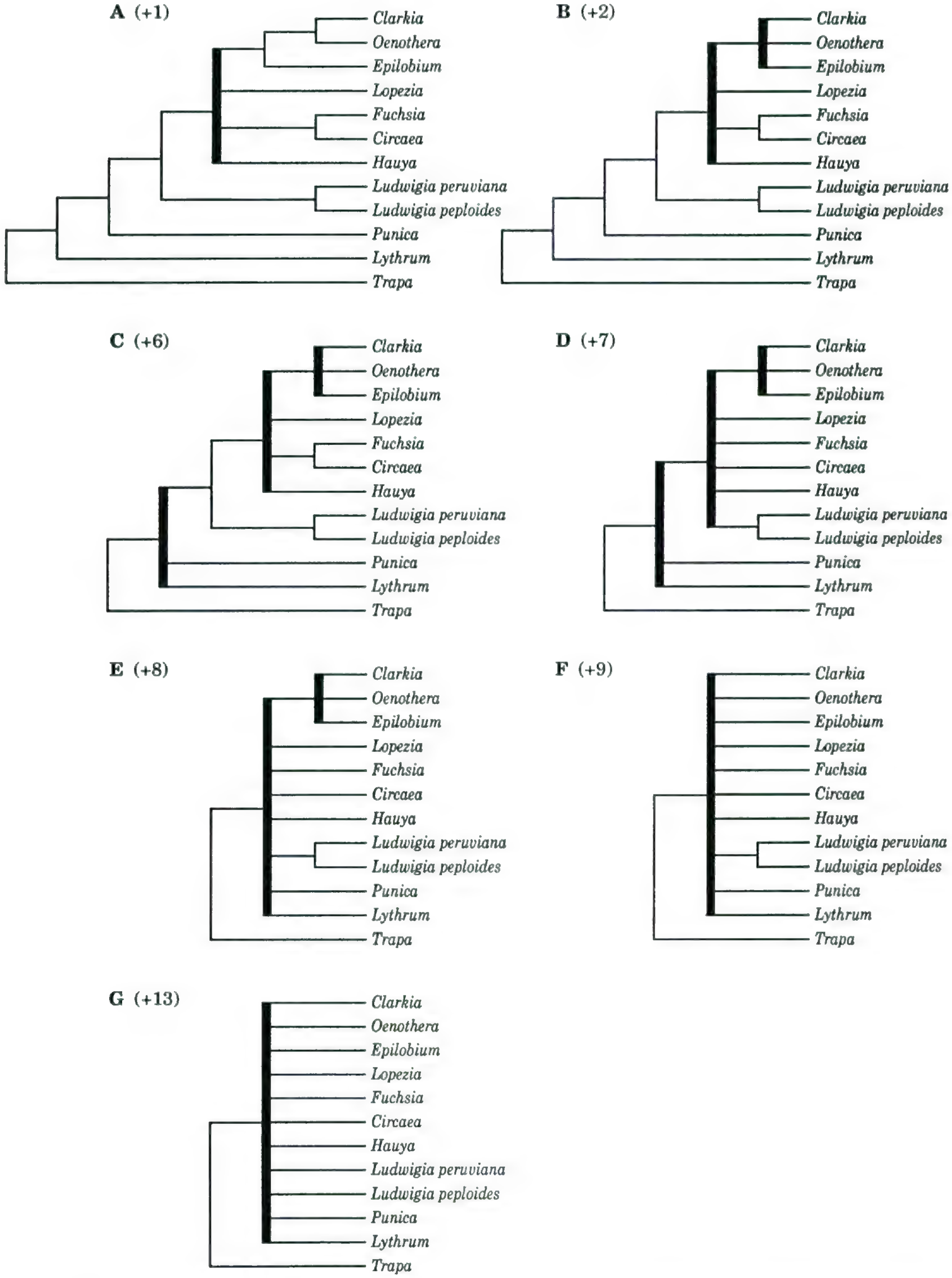


FIGURE 2. Decay analysis of the most parsimonious, 168-step tree. The number of extra steps at which each clade decays is reported in parentheses. Solid bars indicate the polytomies formed by the collapse of each monophyletic group in trees longer than the 168-step tree.

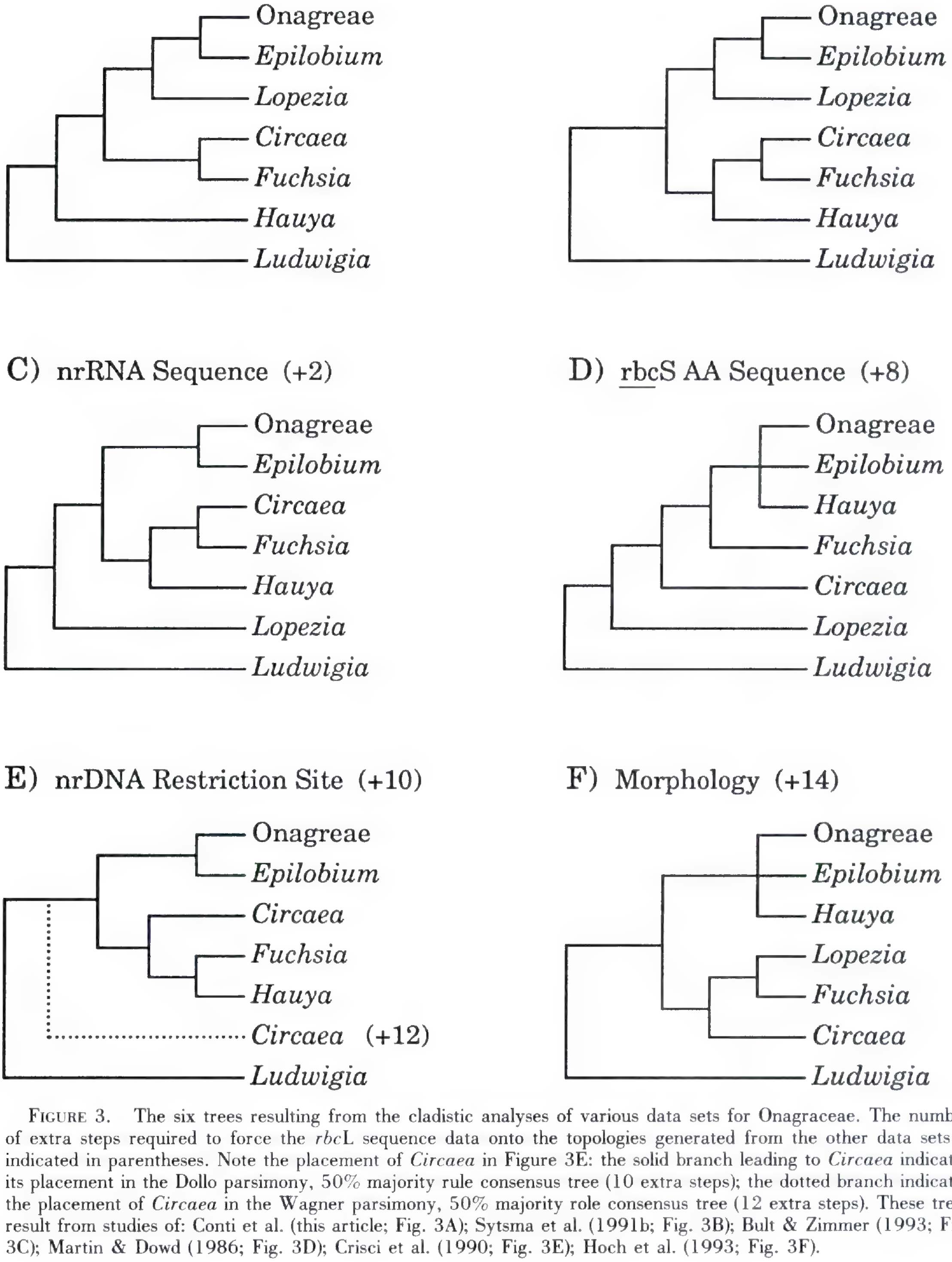


FIGURE 3. The six trees resulting from the cladistic analyses of various data sets for Onagraceae. The number of extra steps required to force the *rbc*L sequence data onto the topologies generated from the other data sets is indicated in parentheses. Note the placement of *Circaea* in Figure 3E: the solid branch leading to *Circaea* indicates its placement in the Dollo parsimony, 50% majority rule consensus tree (10 extra steps); the dotted branch indicates the placement of *Circaea* in the Wagner parsimony, 50% majority role consensus tree (12 extra steps). These trees result from studies of: Conti et al. (this article; Fig. 3A); Sytsma et al. (1991b; Fig. 3B); Bult & Zimmer (1993; Fig. 3C); Martin & Dowd (1986; Fig. 3D); Crisci et al. (1990; Fig. 3E); Hoch et al. (1993; Fig. 3F).

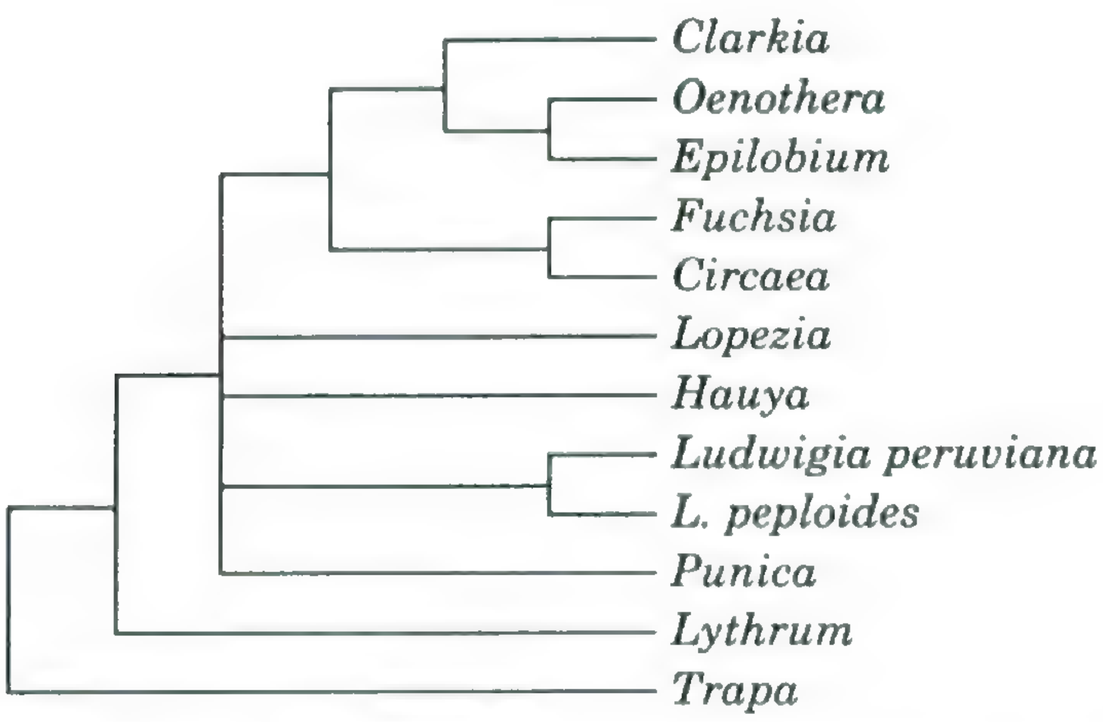


FIGURE 4. Strict consensus tree of the four most parsimonious trees resulting from elimination of third codon positions in *rbc*L sequences.

parisons of congruence between the single *rbc*L tree and those generated from a variety of other data sets, both molecular and morphological.

### 1. INTERTRIBAL RELATIONSHIPS IN ONAGRACEAE

The Fitch tree (Fig. 1) strongly supports three monophyletic tribal groups within the family: (i) all tribes except Jussiaeeae; (ii) Fuchsieae and Circaeeae; (iii) Onagreae and Epilobieae. The placements of Hauyeae and Lopezieae are less well supported. The most parsimonious *rbc*L tree agrees with all other data sets (Fig. 3) in placing *Ludwigia* (sole genus of the tribe Jussiaeeae) as sister to all other Onagraceae (with a bootstrap value of 100%, 11 informative characters, seven of which are consistent, and a decay index of 13).

*Ludwigia* appears to retain a number of plesiomorphic morphological features, including presence of up to seven parts in the floral whorls, as opposed to the typical four-merous flowers of the other Onagraceae (Eyde, 1981, 1982; Hoch et al., 1993), massive, ovuliferous placentas, minor vascular bundles, and absence of a constriction in the floral tube beyond the ovary. *Ludwigia* shares the plesiomorphic *Met-Lys* N-terminal amino acids of the nuclear-encoded *rbc*S polypeptide with all other angiosperm taxa (mostly from Myrtales) analyzed by Martin & Dowd (1986), whereas the rest of Onagraceae are clearly set apart from *Ludwigia* by the distinctive and synapomorphic *Phe-Asn* N-terminus.

*Ludwigia* is also distinguished from the rest of Onagraceae by autapomorphies, most notably the unique nectary position. The location of the nectaries of *Ludwigia* around the base of the style, inside the anthers (instead of on the floral tube, outside the anthers, as in all other Onagraceae), induced Eyde to conclude that epigyny evolved independently in the two main evolutionary lines of Onagraceae, namely *Ludwigia* and the rest of the family (Eyde, 1982; Raven, 1988).

A major achievement of the *rbc*L sequence data in elucidating the relationships among tribes in Onagraceae is the definition of the clade Fuchsieae–Circaeeae. *Fuchsia* and *Circaea* are quite distinctive morphologically. *Fuchsia* is generally shrubby or treelike, mostly with large, bird-pollinated flowers, and has a Gondwanaland distribution (although with some distinctive sections in North America: Berry, 1982; Raven, 1979, 1988). *Circaea*, on the other hand, is herbaceous, small-flowered, fly-pollinated, and has a Laurasian distribution. Morphologically the two genera each exhibit numerous autapomorphies, share none or a few derived states with other tribes, and are thus not linked in phylogenetic analyses of morphological characters (Hoch et al., 1993). Additionally, if one considers the relatively low sequence divergence (1.7%) between Circaeeae and Fuchsieae (versus 1.9% between *Clarkia* and *Oenothera* in the tribe Onagreae: see Table 3), the implications of these results with respect to biogeography and perhaps rates of morphological divergence are considerable.

The woody *Fuchsia* lineage has undergone a seven- to eleven-fold slowdown in *rbc*L sequence divergence relative to the herbaceous *Circaea* lineage (with DELTRAN and ACCTRAN transformations, respectively; see Fig. 1). A low amount of chloroplast DNA divergence (as measured by *P* values using restriction site data) between two, morphologically distinct species of *Fuchsia* (a tree versus a scrambling liana) has already been noted (Sytsma et al., 1991a; Sytsma & Smith, 1992). *Fuchsia* and *Hauya*, the other genus of Onagraceae that includes shrubs and trees, actually show the lowest amount of intertribal *rbc*L sequence divergence (1.4%; see Table 3), even though they are not supported as a clade. Both tribes have few autapomorphies not due to homoplasy (two in *Fuchsia*, four in *Hauya*; see Fig. 1). The apparent slow rate of *rbc*L sequence divergence in both the woody Fuchsieae and Hauyeae is also reminiscent of that reported for the Palmae (Wilson et al., 1990).

The third well supported clade includes Onagreae (nine genera) and Epilobieae. These two tribes exhibit many more apomorphic features than do the other tribes (Raven, 1979, 1988; Hoch et al., 1993). The derived nature of these two tribes is suggested by their placement in a terminus of the *rbc*L phylogram (Fig. 1).

Within the Onagreae–Epilobieae clade, the

branch supporting the monophyly of Onagreae (represented by *Clarkia* and *Oenothera*) is not very robust (Figs. 1, 2B). The weak support of the monophyly of Onagreae is reflected in the *rbc*S amino acid sequence tree (Fig. 3D) and the morphology tree (Fig. 3F: strict consensus tree of the seven most parsimonious trees), which both place the Onagreae in an unresolved trichotomy with Epilobieae and Hauyeae.

Raven (1979) indicated that *Clarkia* (now including *Heterogaura*; see Lewis & Raven, 1992), as well as *Epilobium*, share derived character states, unique in the family, such as a dry, papillate stigma and four-lobed stigmas with the lobes in the commissural position. The presence of commissural stigmas was explained by Eyde (1982) as related to the evolution of protandry in these two genera. Further sampling of Onagreae and Epilobieae for *rbc*L sequence data would furnish an independent test for the possible paraphyly of Onagreae (Raven, 1979; Hoch et al., 1993) and for the phylogenetic interpretation of these unique morphological characters (Baum & Larson, 1991; Coddington, 1988).

The placement of Hauyeae between Jussiaeeae and the rest of Onagraceae is the weakest branch of the *rbc*L tree, with a low bootstrap value (44%), five synapomorphies (only two of which are consistent), and the collapse to a polytomy at just one extra step from the shortest tree (Fig. 2A). *Calylophus* and *Gaura* (both Onagreae; chromosome number $x = 7$) share some apparently derived embryological features with the otherwise generalized *Hauya*, which has the basic chromosome number $x = 10$.

The second weakest branch in the *rbc*L Wagner tree is the placement of *Lopezia* as the sister group of Onagreae–Epilobieae, supported by five synapomorphies, of which only two are consistent.

## 2. CONGRUENCE WITH OTHER CLADISTIC ANALYSES

The picture of phylogenetic relationships within Onagraceae resulting from the *rbc*L sequence data can be compared with the evolutionary scenarios provided by both molecular and morphological studies (see Hillis, 1987; Sytsma, 1990; Donoghue & Sanderson, 1992).

The placement of Hauyeae between Jussiaeeae and the rest of Onagraceae as seen in the *rbc*L tree is incongruent with the cpDNA restriction site tree and the nrRNA sequence tree, which are indicated as the closest to the *rbc*L cladogram (respectively at one and two extra steps) by the analysis of constrained trees (Fig. 3). The cpDNA and the nrRNA trees agree in placing Hauyeae as the sister tribe to the clade Fuchsieae–Circaeeae. The nrDNA restriction site tree does not corroborate the topology of the nrRNA sequence tree, in that the former places Hauyeae as the sister tribe to Fuchsieae. Both morphological and *rbc*S amino acid sequence data indicate that Hauyeae, Onagreae, and Epilobieae form a tight group (Fig. 3D, F).

The *rbc*L sequence data corroborate the cpDNA restriction site data (Sytsma et al., 1991b) and the nrRNA sequence data (Bult & Zimmer, 1993) in defining the Fuchsieae–Circaeeae clade. In the nrRNA sequence tree, however, the Fuchsieae Circaeeae clade is less robust than in the *rbc*L tree, since it is supported by only four synapomorphies, three of which are homoplasious. There is no agreement concerning the phylogenetic relationships of *Fuchsieae* and *Circaeeae* among the nrDNA tree, the *rbc*S tree, and the morphological tree. The placement of Circaeeae in the two consensus trees resulting from nrDNA restriction site data is unstable. In fact, the 50% majority rule consensus tree based on Dollo parsimony indicates Circaeeae as the sister tribe to the clade Fuchsieae–Hauyeae, whereas the consensus tree based on Wagner parsimony places Circaeeae as the intermediate tribe between Jussiaeeae and the rest of Onagraceae (see Fig. 3E).

There is agreement between the *rbc*L sequence tree (Fig. 3A) and the cpDNA restriction site tree (Fig. 3B), both maternal trees, in indicating Lopezieae as the sister tribe to the clade Onagreae Epilobieae. On the other hand, the two nuclear genome trees, based on nrRNA nucleotide and *rbc*S amino acid sequence data, place *Lopezia* between *Ludwigia* and the rest of Onagraceae. The morphological tree defines Lopezieae as the sister tribe to Fuchsieae on the basis of a single trait (lack of starchy pollen). No nrDNA restriction site data are available for Lopezieae. The shifting placements of Lopezieae in the trees resulting from different data sets, especially the discrepancy between the two maternal and the two biparental trees, suggest the possible occurrence of ancient chloroplast capture in this tribe (see Smith & Sytsma, 1990; Rieseberg & Brunsfeld, 1992). Further sampling of the genus for *rbc*L sequences and additional sequence data of nuclear genes may help to resolve the relationships of Lopezieae with the rest of the family.

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# NUCLEOTIDE SEQUENCES OF THE *rbc*L GENE INDICATE MONOPHYLY OF MUSTARD OIL PLANTS[1]

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ABSTRACT

Nucleotide sequences for the chloroplast *rbc*L gene were obtained from representatives of 11 of the 15 plant families known to produce glucosinolates (mustard oil glucosides). Parsimony analyses indicate that these constitute two widely separated groups and thus imply two independent origins of the mustard oil/myrosin cell syndrome. A strongly supported, major group comprises the mustard family Brassicaceae and its near relatives Capparaceae, Resedaceae, and Tovariaceae along with such morphologically diverse taxa as Bataceae, Bretschneideraceae, Caricaceae, Limnanthaceae, Moringaceae, and Tropaeolaceae. The second mustard oil group is restricted to the euphorbiaceous genus *Drypetes*. *Akania*, the subject of an independent *rbc*L analysis, pairs with *Bretschneidera*, and these are collateral with *Tropaeolum* at the base of the major mustard oil clade. Gyrostemonaceae, *Pentadiplandra*, and Salvadoraceae have not been analyzed for *rbc*L sequences. The gene data corroborate many aspects of Rodman's recent cladistic analysis based predominantly on morphological characters; together the molecular and morphological evidence support Dahlgren's radical classification of an expanded order Capparales.

Flowering plants produce a remarkable array of so-called secondary metabolites, e.g., alkaloids, cyanogens, mustard oils, and phenolics. Such natural products often have beneficial (spices, medicinals) or deleterious (allergens, poisons) effects on humans. The evolutionary origins and diversification of secondary metabolites are poorly known, with instances of parallel or convergent evolution suspected for many of them (Giannasi & Crawford, 1986). Their use as taxonomic markers (often under the rubric of "micromolecular characters") is widespread and of long standing, but it raises a suspicion of circularity. Classification schemes, interpreted as evolutionary scenarios, are used to explain the origins and changes in micromolecules, which may have been incorporated into the database used to construct those very classifications. An independent set of characters is required to evaluate the phylogenetic utility and reliability of micromolecular data.

Mustard oil glucosides or glucosinolates, the compounds that release distinctive pungent principles in radish, mustard, and capers (Fenwick et al., 1983), provide a classic example of taxonomically useful micromolecules (Ettlinger & Kjaer, 1968; Kjaer, 1973; Rodman, 1991a, b). Characteristic of 14 families of dicots and of the genus *Drypetes*, usually allied with Euphorbiaceae, the compounds are structurally diverse and amenable to rapid chromatographic analysis (Rodman, 1978, 1981). They are demonstrably useful as population- and species-level markers (Al-Shehbaz, 1973; Rodman, 1974; Rodman et al., 1981; Al-Shehbaz & Al-Shammary, 1987) and have been employed in studies of hybridization (Rodman, 1980; Kruckeberg et al., 1982), migration (Rodman, 1976, 1986), and insect–plant interactions (Rodman & Chew, 1980; Louda & Rodman, 1983). The biosynthesis of glucosinolates is known in broad outline and is thought to be a unitary pathway in all these plants (Glover et al., 1988; Boufford et al., 1989). However, little enzymological data exist to evaluate the presumed homology of mustard oil biosynthesis; this is conspicuously so for *Drypetes*, placed in a family otherwise lacking mustard oils but well known for its cyanogenic glycosides (Rodman, 1981).

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TABLE 1. Two recent and contrasting classifications of mustard oil plants, implying either convergence (Cronquist, 1981, 1988) or unique origin/parallelism (Dahlgren, 1975a, 1977) for the mustard oil/myrosin cell syndrome. Where nonglucosinolate families are included in the order, an "etc." follows the name of the glucosinolate taxa. *Drypetes* (including *Putranjiva*) is the only genus of Euphorbiaceae known to produce glucosinolates. Both authors associate the genus *Pentadiplandra* with the family Capparaceae (treated as a separate family in Rodman, 1991a, b).

| Cronquist (1981, 1988) | Dahlgren (1975a, 1977) |
|---|---|
| Capparales—Brassicaceae, Capparaceae, Resedaceae, Moringaceae, Tovariaceae. | Capparales—Brassicaceae, Capparaceae, Resedaceae, Moringaceae, Tovariaceae, Bataceae, Gyrostemonaceae, Salvadoraceae, Limnanthaceae, Tropaeolaceae, and Bretschneideraceae. |
| Batales—Bataceae and Gyrostemonaceae. | |
| Violales—Caricaceae, etc. | Violales—Caricaceae, etc. |
| Celastrales—Salvadoraceae, etc. | |
| Euphorbiales—*Drypetes*, etc. | Euphorbiales—*Drypetes*, etc. |
| Sapindales—Akaniaceae, Bretschneideraceae, etc. | Sapindales—Akaniaceae, etc. |
| Geraniales—Limnanthaceae, Tropaeolaceae, etc. | |

Mustard oils are typically accompanied by a unique catabolic enzyme called myrosinase (Bones et al., 1991), which is sequestered or concentrated in specialized idioblasts known as myrosin cells (Jørgensen et al., 1977; Jørgensen, 1981). The origin and taxonomic distribution of the glucosinolate-myrosinase trait present a challenging question: Has glucosinolate biosynthesis evolved once or repeatedly? Are the mustard oil plants a monophyletic lineage or a polyphyletic assemblage?

The classification of mustard oil plants has attracted the attention of numerous phylogenetically inclined taxonomists. Rodman (1991a) identified 18 different schemes published in the 20th century, three of which have been discussed in detail for their bearing on glucosinolate evolution (Rodman, 1981). Two of these classifications (Table 1) provide contrasting end-points on the spectrum of recent taxonomic interpretation of these plants: Cronquist (1981, 1988) and Dahlgren (1975a, 1977). Cronquist's view, shared probably by a majority of taxonomists, would imply convergence for glucosinolates in several orders of his dicot subclasses Dilleniidae and Rosidae. To force an interpretation of unique origin in the context of Cronquist's classification would necessitate multiple instances of biosynthetic loss or repression in numerous lineages. Dahlgren, in contrast, lumped most mustard oil taxa into a single large order Capparales, excluding only *Akania*, Caricaceae, and the genus *Drypetes* of Euphorbiaceae. He placed Caricaceae in an order Violales that he affiliated with Capparales, and in turn he allied these with Euphorbiales. Dahlgren (1975a, 1977) originally associated *Akania* with Sapindales but later (Dahlgren et al., 1981) suggested an affiliation with Caricaceae. Thus, Dahlgren's scheme permits the interpretation that glucosinolate biosynthesis arose once in a stem lineage to these three orders with subsequent loss or repression in the remaining Violales and in all Euphorbiales except *Drypetes*. An alternative evolutionary scenario from Dahlgren's classification would postulate two or three parallel origins within a closely related group of dicots (Rodman, 1981). Although Dahlgren (1980, 1983) later retreated from his original view of an expanded Capparales, the earlier classification provides a striking contrast to the convergence and polyphyly implied by so many traditional schemes such as Cronquist's.

Recent cladistic and phenetic studies of mustard oil taxa provide the first explicit evaluation of variant classifications of these plants (Rodman, 1991a, b). Ninety characters were assembled for the cladistic analysis, including anatomical and morphological (vegetative and reproductive), chromosomal, palynological, phytochemical, and ultrastructural features; morphological characters, broadly defined, predominated in this data set. The results were in striking agreement with Dahlgren's (1975a, 1977) broad concept of an expanded order Capparales. A clade of core Capparales (Brassicaceae, Capparaceae, Resedaceae, and Tovariaceae) was joined with Gyrostemonaceae and in turn allied with Bataceae, Salvadoraceae, and the nonglucosinolate *Koeberlinia*. Diagnostic features for this group include: vestured pitting; curved embryo in seed; dilated cisternae of the endoplasmic reticulum; floral tetramery; myrosin cells; and glucosinolates of several biosynthetic types. On the basis of less compelling character evidence, the clade was joined successively by: sister taxa Moringaceae + Tropaeolaceae; then sister taxa *Akania* + *Bretschneidera*; and then sister taxa Caricaceae + *Pentadiplandra*. Cladistic linkages among the mustard oil taxa held whether glucosinolates were

incorporated as characters into the analysis or not. *Drypetes* remained the most distant mustard oil taxon. Limnanthaceae, linked to Balsaminaceae, provided a second likely instance of convergence for glucosinolates.

An independent evaluation of taxonomic relationships of mustard oil plants is here provided by a comparative analysis of nucleotide sequences from the chloroplast gene for the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (*rbc*L). Theoretical and practical reasons for the phylogenetic value of *rbc*L have been discussed (Ritland & Clegg, 1987; Palmer et al., 1988; Clegg & Zurawski, 1992), and an increasing number of empirical studies attests to the utility of *rbc*L sequence data (Doebley et al., 1990; Soltis et al., 1990; Les et al., 1991; Donoghue et al., 1992; Giannasi et al., 1992; Kim et al., 1992; Olmstead et al., 1992; Rettig et al., 1992). Gene sequence data provide a large number of variable, homologous characters (nucleotide site positions) that promise ample resolving power across a broad range of taxa. Three assumptions are here made in accepting *rbc*L sequence data as informative about plant phylogeny: (1) the *rbc*L gene is representative of the plant's genome, at least the (often) maternally inherited chloroplast component; (2) nucleotide site differences among the taxa reflect a conservative history of evolutionary change, with parallel or convergent mutations not great enough to obscure phylogenetic linkages; and (3) one or two taxa can represent large families because sequence differences within families are less than those between families. In the long run these assumptions will be evaluated against our increasing knowledge of plant genome diversity.

## Materials and Methods

For our study, *rbc*L nucleotide sequences of ca. 1,400 bases each were assembled for 33 taxa. Nine of these are here reported as new: *Bretschneidera sinensis*, *Capparis hastata*, *Carica papaya*, *Cleome hasleriana*, *Drypetes roxburghii*, *Koeberlinia spinosa*, *Moringa oleifera*, *Reseda alba*, and *Tovaria pendula*. Four published sequences were drawn from GenBank (Bilofsky et al., 1986): *Amaranthus hypochondriacus*, *Gossypium hirsutum*, *Plumbago capensis*, and *Spinacia oleracea*. The rest were either generously provided by others or are published elsewhere (Table 2). Ten of the known glucosinolate-producing families plus the genus *Drypetes* are represented in our analysis. *Akania* is the subject of an independent *rbc*L report (Gadek et al., 1992). The remaining mustard oil taxa, Gyrostemonaceae, Pentadiplandraceae, and Salvadoraceae, have not been sequenced. *Koeberlinia*, usually allied with Capparaceae, has been reported to develop myrosin cells (Gibson, 1979); it has been analyzed for glucosinolates but with negative results (Ettlinger & Kjaer, 1968; Rodman, 1981). Here it is treated as its own family (see Rodman, 1991a, b). Recently, the thiocyanate or isothiocyanate breakdown products of presumptive parent glucosinolates were reported from two species of *Phytolacca* (Phytolaccaceae) and from one of *Bursaria* of Pittosporaceae (Daxenbichler et al., 1991). If confirmed, these would constitute novel and remarkable additions to the list of known mustard oil taxa (Ettlinger, 1987; Rodman, 1991a). Until such confirmation, however, caution is justified. Claims of glucosinolates in Plantaginaceae (Cole, 1976) and in Sterculiaceae (Gill et al., 1984) have been disputed (Larsen et al., 1983; Bjerg et al., 1987, respectively) and remain unconfirmed. None of these families is represented in our study (but see Chase et al., 1993).

For eight of the nine new sequences, methods of analysis were as follows (for *Koeberlinia spinosa* methods are described by Price & Palmer, 1993; GenBank accession numbers for the nine new sequences reported here are listed in Table 2). Total genomic DNA was extracted from fresh or frozen leaves (or green twigs for *Koeberlinia*) by a modified hot CTAB procedure (Doyle & Doyle, 1987). Polymerase chain reaction (PCR) using commercial "AmpliTaq" enzyme kits (see Erlich, 1989; Williams, 1989) and a Perkin-Elmer Cetus Thermal Cycler were employed to amplify the *rbc*L DNA, making use of flanking 5′ and 3′ primers provided by Richard Olmstead. The forward 5′ primer extends 26 bases into the presumptive coding region of the gene from the AUG start codon; consequently, that 26-mer portion of our new sequences was coded as blank for the computer analyses. The resulting PCR product was cleaned with commercial "Gene-Clean" and aliquots were run on short 1.0% agarose gels to confirm the presence of a single band at ca. 1.4 kilobases when visualized by staining with ethidium bromide under ultraviolet light.

Direct dideoxy sequencing from the double-stranded PCR product was done using a modification of published methods (Korneluk et al., 1985; Zhang et al., 1988; Kusukawa et al., 1990) developed by Elena Conti (Conti et al., 1993). We used commercial "Sequenase Version 2.0" kits with sulfur-35 radiolabelled dATP in concert with internal forward and reverse primers made available by Gerard Zurawski. About half the complete sequence from forward primers was confirmed by using reverse primers. Products of the sequencing

TABLE 2. Sources of *rbc*L nucleotide sequences for mustard oil taxa (marked by an asterisk: Ettlinger, 1987; Rodman, 1991a) and putative relatives, arranged according to Cronquist's (1981) system (except for Koeberliniaceae).

I. Caryophyllidae

Caryophyllales (Centrospermae)
- Amaranthaceae, *Amaranthus hypochondriacus*, Michalowski et al., 1990.
- Chenopodiaceae, *Spinacia oleracea*, Zurawski et al., 1981.

Plumbaginales
- Plumbaginaceae, *Plumbago capensis*, Giannasi et al., 1992.

II. Dilleniidae

Batales
- Bataceae, **Batis maritima*, James Manhart & Jeff Rettig, unpublished.

Capparales
- Brassicaceae, **Brassica juncea*, Jackie Nugent, unpublished.
- Capparaceae, **Capparis hastata, Iltis 30315* (WIS), GenBank M95754; **Cleome hasleriana, Al-Shehbaz s.n.* (MO), GenBank M95755.
- Koeberliniaceae, *Koeberlinia spinosa, Al-Shehbaz s.n.* (MO), GenBank L14600.
- Moringaceae, **Moringa oleifera, Iltis 30501* (WIS), GenBank L11359.
- Resedaceae, **Reseda alba*, commercial seed, GenBank M95756.
- Tovariaceae, **Tovaria pendula, D. Smith & J. F. Smith 1831* (WIS), GenBank M95758.

Malvales
- Malvaceae, *Gossypium hirsutum*, Gulov et al., 1990.

Violales
- Caricaceae, **Carica papaya*, WIS Botanical Garden, GenBank M95671.
- Passifloraceae, *Passiflora quadrangulata*, Chase et al., 1993.

III. Rosidae

Euphorbiales
- Euphorbiaceae, **Drypetes roxburghii*, Lyon Arboretum, Hawaii, GenBank M95757; *Euphorbia polychroma*, Chase et al., 1993.

Geraniales
- Balsaminaceae, *Impatiens biflora*, Chase et al., 1993.
- Geraniaceae, *Geranium grandiflorum*, *Pelargonium* × *hortorum*, Price & Palmer, 1993.
- Limnanthaceae, **Floerkea proserpinacoides*, Chase et al., 1993; **Limnanthes douglasii*, Price & Palmer, 1993.
- Oxalidaceae, *Oxalis dillenii*, Price & Palmer, 1993.
- Tropaeolaceae, **Tropaeolum majus*, Price & Palmer, 1993.

Myrtales
- Combretaceae, *Quisqualis indica*, Chase et al., 1993.
- Lythraceae, *Lythrum subsessilifolium*, Conti et al., 1993.
- Onagraceae, *Clarkia xantiana*, Conti et al., 1993.

Polygalales
- Vochysiaceae, *Qualea* sp.?, Chase et al., 1993.

Rosales
- Saxifragaceae, *Heuchera micrantha*, *Penthorum sedoides*, Soltis et al., 1990.

Sapindales
- Aceraceae, *Acer saccharum*, Chase et al., 1993.
- Akaniaceae, **Akania bidwillii*, Gadek et al., 1992.
- Bretschneideraceae, **Bretschneidera sinensis, Leu & Lin 726* (WIS), GenBank M95753.
- Burseraceae, *Bursera inaguensis*, Chase et al., 1993.
- Simaroubaceae, *Ailanthus altissima*, Chase et al., 1993.

reactions were run on 6% polyacrylamide gels or on commercial 5% "Long Ranger" gels, and the results were visualized by autoradiography. Sequences were read and base changes coded by hand against a tobacco *rbc*L template. Sequences were entered into the University of Wisconsin Genetics Computer Group package of programs (Devereux et al., 1984) to check for protein translation and internal restriction enzyme sites as a test of sequence authenticity.

For phylogenetic analysis of the sequence data, we created a matrix of 33 taxa and 1,428 characters, choosing to terminate the *rbc*L sequence at position 1428 in order to maintain conformity with the general analysis (Chase et al., 1993). Also, sequences beyond position ca. 1430 were variable and difficult to align, whereas alignment was easily done by inspection for the rest of the gene.

Phylogenetic relationships were inferred using a maximum parsimony strategy implemented with Swofford's PAUP computer programs (Swofford, 1991; see Sanderson, 1990); these generate "Fitch" parsimony trees with unordered nucleotide data (Fitch, 1971). Results are thus directly comparable to those derived from the predominantly morphological data set analyzed with PAUP in the recent cladistic study (Rodman, 1991b). We used the TBR and MULPARS options in our search procedure. We are aware of controversies over the best methods of estimating or inferring phylogenetic relationships (Sober, 1988; Swofford & Olsen, 1990); nevertheless, we consider the maximum parsimony approach to be reasonable and defensible (see Hillis et al., 1992). Sequences from 13 mustard oil taxa are included in our data set, usually one genus per family. Both genera of Limnanthaceae, *Floerkea* and *Limnanthes*, are in-

cluded; we are not aware of any published confirmation of glucosinolates in *Floerkea*, but the fresh leaves produce a mild "horseradish" taste when chewed from which we infer their presence. To these we added sequences from 20 putative relatives or outgroups. With the many potential outgroups treated here, we adopted a strategy of "simultaneous resolution" (Maddison et al., 1984); this avoids the assumption that mustard oil taxa must form a monophyletic group. Three considerations affected our choices of outgroup taxa. (1) We wanted to evaluate traditional taxonomic relationships for various mustard oil plants (e.g., *Batis* allied with centrosperms; *Bretschneidera* allied with Sapindales; Caricaceae allied with Violales such as Passifloraceae; Limnanthaceae and Tropaeolaceae allied with Geraniaceae and/or Balsaminaceae; *Drypetes* allied with Euphorbiaceae). (2) We wished to take advantage of results from prior studies (Olmstead et al., 1992) and from the general *rbc*L analysis (Chase et al., 1993) that suggested malvalean and sapindalean affinities with Capparales. (3) We wanted to use several outgroup taxa in order to avoid artifactual linkages induced by distant or isolated taxa, the "long edges [branches] attract" effect (Hendy & Penny, 1989).

The robustness of resulting trees was evaluated in various ways: bootstrapping (Felsenstein, 1985; Sanderson, 1989) with PAUP's heuristic search algorithm; "decay analysis" (Bremer, 1988; for an example see Smith & Sytsma, 1990) to explore the topology of trees one to several steps longer than the most parsimonious trees found under the heuristic search procedure; and a branch-and-bound exhaustive search with a reduced set of 14 taxa. A codon-position weighting scheme, with weights and stepmatrix values calculated by Albert et al. (1993), was also used with the PAUP-heuristic search. The scheme differentially weights changes at first, second, and third codon positions, relying upon ratios derived empirically from a large data set of protein-coding genes. When consensus trees were generated, the strict ("Nelson") consensus option was used (Swofford, 1985: CONTREE documentation) unless otherwise noted.

## Results

With the PAUP-heuristic search procedure and with *Heuchera* and *Penthorum* (Saxifragaceae) selected as outgroups, we obtained two equally parsimonious trees with the unweighted data, of length = 1,604 steps or site changes and with a consistency index (Kluge & Farris, 1969) of 0.39 (excluding unique substitutions). These are reasonable outgroup choices in light of results from the general *rbc*L study (Chase et al., 1993) that place them in a clade collateral to all mustard oil taxa and their near relatives. Figure 1A shows the two equally parsimonious trees. Numbers of nucleotide substitutions (branch lengths) are indicated for the topology that matches the single tree obtained by the weighted analysis; with the better f-ratio (= 0.2995; see Swofford & Maddison, 1987) this is our preferred tree of the two. All the mustard oil taxa form a monophyletic lineage excepting only *Drypetes*, which links near *Euphorbia* and *Passiflora*. The sister group to the major mustard oil clade is an alliance of malvalean (*Gossypium*) and sapindalean taxa (*Acer*, *Ailanthus*, *Bursera*) as discovered in recent analyses (Olmstead et al., 1992; Chase et al., 1993). There are 522 variable site positions for these taxa, of which 351 (or 25% of the 1,428 sites) provide cladistically informative changes.

Several results appear noteworthy, the first two being in accord with traditional taxonomic judgments, but all the rest contrary to traditional alignments. (1) Brassicaceae, Capparaceae, Resedaceae, and Tovariaceae are closely related and form what can be called "core Capparales." (2) *Drypetes* links near *Euphorbia* and *Passiflora* and not close to other mustard oil taxa. (3) Limnanthaceae fall within the major glucosinolate clade and do not link with either Balsaminaceae (represented by *Impatiens*) or Geraniaceae (represented by sister taxa *Geranium* + *Pelargonium*; see Price & Palmer, 1993). (4) *Batis* falls within the major glucosinolate clade and does not link with either Centrospermae (represented by sister taxa *Amaranthus* + *Spinacia*) or sapindalean taxa. (5) *Bretschneidera* links near the base of the glucosinolate clade and not with Sapindales (represented by *Acer*, *Ailanthus*, and *Bursera*). (6) *Carica* links near the base of the glucosinolate clade and not with Violales (represented by *Passiflora*). (7) *Tropaeolum* also links near the base of the glucosinolate clade and not with Geraniaceae or Oxalidaceae (represented by *Oxalis*; see Price & Palmer, 1993). All but one of these findings are corroborated by the recent cladistic analysis based on a predominantly morphological data set (Rodman, 1991b).

To assess the robustness of these findings, we ran the PAUP-bootstrap procedure (Swofford, 1991) and performed decay analyses (Donoghue et al., 1992) to accumulate trees one to five steps longer than the two parsimonious trees originally obtained. The decay values were obtained by holding all trees of 1,609 steps and fewer using PAUP; these trees were then sequentially filtered one step

shorter at a time, and with each filter a strict consensus tree was generated. Branches that did not collapse at 1,609 steps were scored as greater than +5 steps. Figure 1B presents bootstrap results (as percentages of 100 replicates) and the number of steps (additional nucleotide substitutions) required to collapse each node for our preferred tree. At 1,609 steps (+5 changes) there were 2,319 trees; 1,608 (+4) there were 905; 1,607 (+3) there were 320; 1,606 (+2) there were 98; and at 1,605 steps (+1) there were 21. We did not pursue decay analyses beyond five steps because the computations require too much time. The major mustard oil clade is strongly supported with a bootstrap value of 93% and a requirement for more than five additional steps to dismember the clade. Likewise, *Drypetes* is strongly allied to *Euphorbia* and *Passiflora* in a separate lineage (bootstrap value = 81%, decay index > 5 steps). Taxon sampling in this portion of our tree is sparse, however, and resolution of the phylogenetic relationships of *Drypetes* will likely require sampling even greater than that summarized in the general analysis (Chase et al., 1993). Within the major glucosinolate clade, strong linkages are shown in the pairing of *Floerkea* + *Limnanthes* (100%), *Bretschneidera* + *Tropaeolum* (98%), and in the clade of Limnanthaceae with *Batis*, *Koeberlinia*, and the core Capparales (99%). Within core Capparales, *rbc*L sequence data provide only weak support for resolution of component families, including the union of Brassicaceae with a paraphyletic Capparaceae [((*Brassica*, *Cleome*), *Capparis*)]. Linkages among nonglucosinolate taxa (e.g., sapindalean, myrtalean, centrospermous) are generally commensurate with results from the general analysis (Chase et al. 1993), but no great emphasis should be placed on our specific results because taxon sampling is sparse.

The robustness of the major glucosinolate clade following bootstrapping and decay analysis encouraged further study of this subset. Designating *Gossypium* as root (the nearest outgroup from the initial analyses), we ran a 14-taxon subset with the branch-and-bound option of PAUP, claimed to guarantee finding the most parsimonious tree if the data set is not too large (Swofford, 1991). A single tree of length = 488 steps and consistency index = 0.59 (excluding autapomorphies) was obtained. The topology was identical to that of the relevant portion of our preferred tree (Fig. 1A) with ingroup relationships fully resolved and with *Bretschneidera* + *Tropaeolum* collateral to the remaining mustard oil taxa. Cladistic relationships among taxa *within* the major glucosinolate clade, therefore, are robust in the face of different outgroup assignments.

## Discussion

Nucleotide sequences from the *rbc*L gene support recognition of a major glucosinolate clade and of a second lineage restricted to the euphorbiaceous genus *Drypetes*. The *rbc*L phylogeny is largely congruent (Fig. 2) with the published cladogram of mustard oil taxa derived from a predominantly morphological character set (Rodman, 1991b, fig. 2). For the core Capparales (Brassicaceae, Capparaceae, Resedaceae, and Tovariaceae) and their sister group (Bataceae + Koeberliniaceae) the two trees are perfectly congruent. The *rbc*L data suggest that Capparaceae are paraphyletic, however; and Gyrostemonaceae and Salvadoraceae remain to be sequenced. At the base of the major glucosinolate clade, sister-group relationships differ between the *rbc*L and morphology trees, with Limnanthaceae (*Floerkea* and *Limnanthes*) presenting the most serious discrepancy.

The unexpected position of Limnanthaceae in the *rbc*L tree is unlikely to reflect misidentifications. Both genera of the family were sequenced (in separate laboratories), the pairing of *Floerkea* and *Limnanthes* is strong (only 17 site differences between them, the smallest in our data set), and their position in the major mustard oil clade is robust. Furthermore, an additional molecular character not included in this analysis supports alliance of Limnanthaceae with Capparales. The *rbc*L gene of *Floerkea* and *Limnanthes* and their sister clade (*Batis* with *Koeberlinia* + core Capparales) does not terminate at position 1428 (as do most other taxa including the basal glucosinolate taxa Caricaceae, Bretschneideraceae, Moringaceae, and Tropaeolaceae) but contains two additional codons before the stop signal. The stop codon, seen in most taxa at positions 1426–1428, has been replaced by one coding for aspartic acid in Limnanthaceae and their sister clade, with subsequent valine (alanine in *Tovaria*) and stop codons. This structural change in the gene ending is not apparent in our data set (because we chose to terminate sequences at 1428), but it is a synapomorphy reinforcing the inclusion of Limnanthaceae within a distinctive glucosinolate subclade. The prior cladistic study (Rodman, 1991b) was interpreted as providing "suggestive but not yet compelling" character evidence for linkage of Limnanthaceae with Balsaminaceae, a traditional taxonomic opinion (Cronquist, 1981, 1988). Bootstrap analysis of the morphology-based result (performed by re-running the data in PAUP-

**1a**

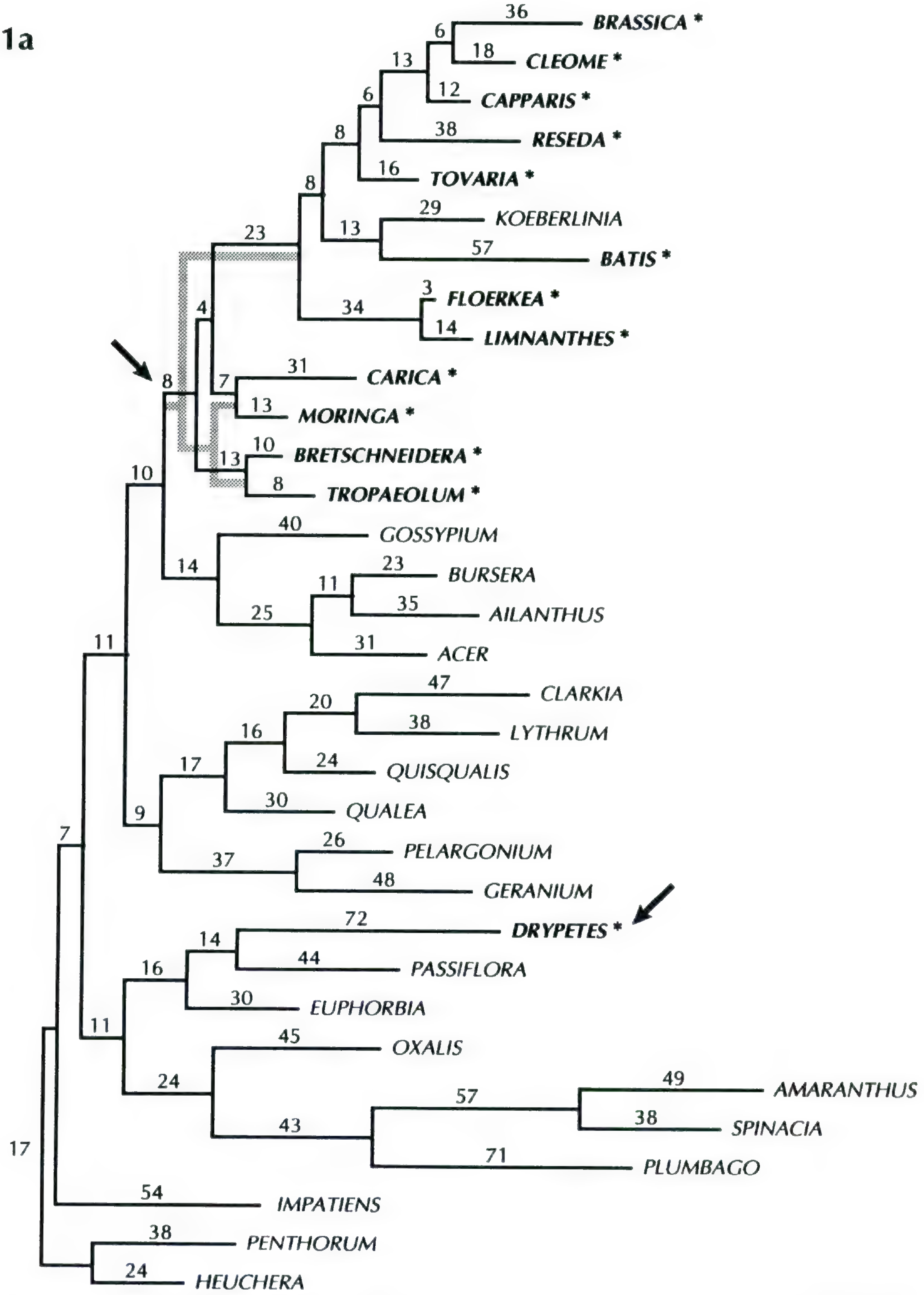


FIGURE 1a. The two equally parsimonious trees for mustard oil taxa (names in boldface marked by asterisks) and putative relatives, of length = 1,604 steps and CI = 0.39, found by analysis of *rbc*L sequences using the PAUP-heuristic search algorithm (ACCTRAN option). The two mustard oil lineages are marked by arrows. The preferred tree, solid lines with branch lengths (number of nucleotide substitutions) above, has the lower f-ratio and is identical in topology with the single tree generated by using the Albert et al. (1993) weighting scheme.

**1b**

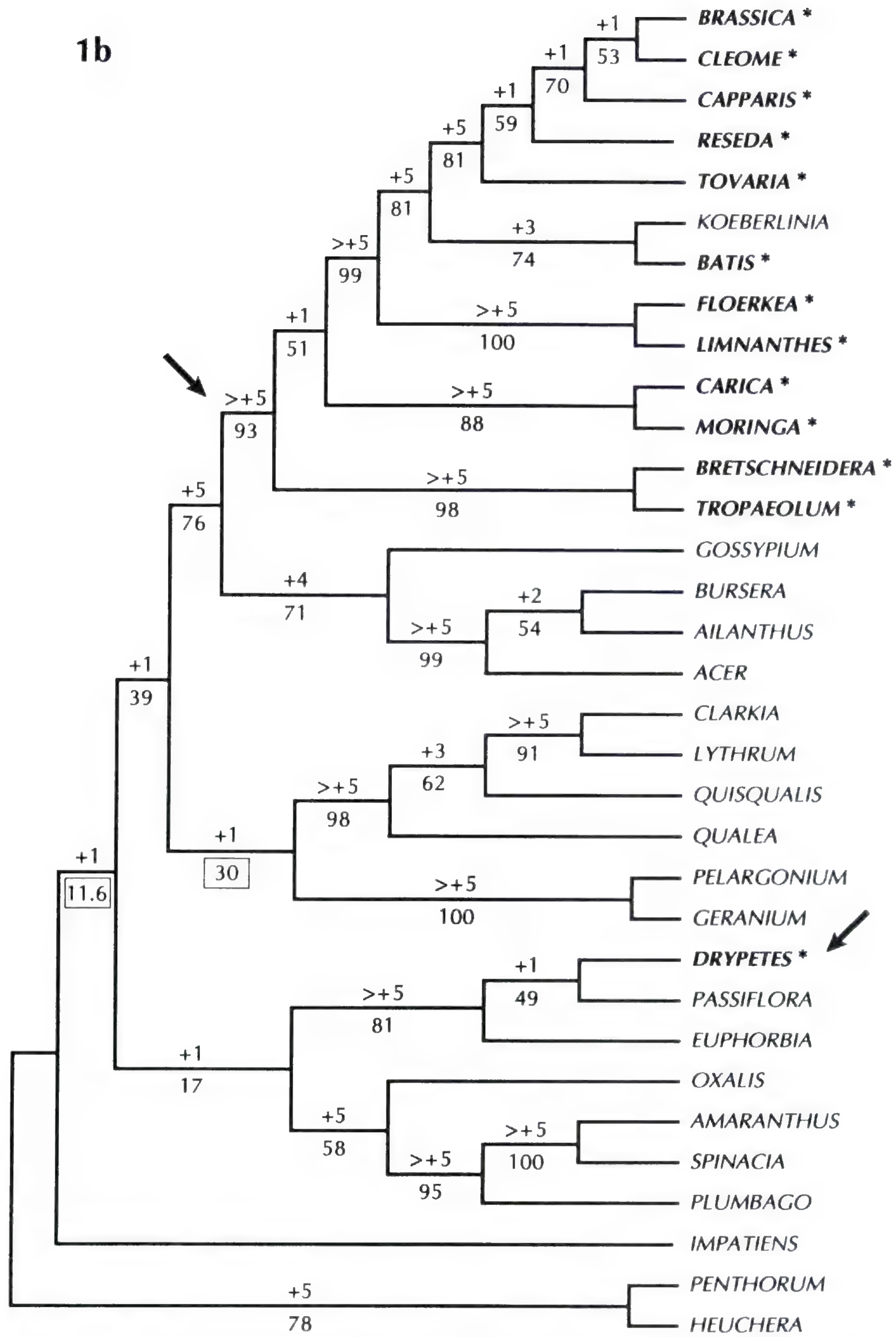


FIGURE 1b. Bootstrap values (percentage of 100 replicates, below branch) and decay index values (number of changes required to collapse the node, above branch) mapped on the preferred parsimonious tree. Asterisks (and boldface) mark mustard oil taxa; arrows indicate the two mustard oil lineages. For two areas with bootstrap values boxed the topology is not in accord with the bootstrap majority-rule consensus tree: in 42% of the replicates myrtalean taxa are collateral to glucosinolate taxa + *Gossypium* + sapindalean taxa; the geranialean taxa are then collateral to all of these with a bootstrap value of 39%. The other discrepancy involves *Impatiens*, which is collateral to the clade of *Drypetes–Euphorbia–Passiflora* in 35% of the bootstrap replicates; this quartet is then collateral to centrosperms + *Oxalis* in 17% of the replicates.

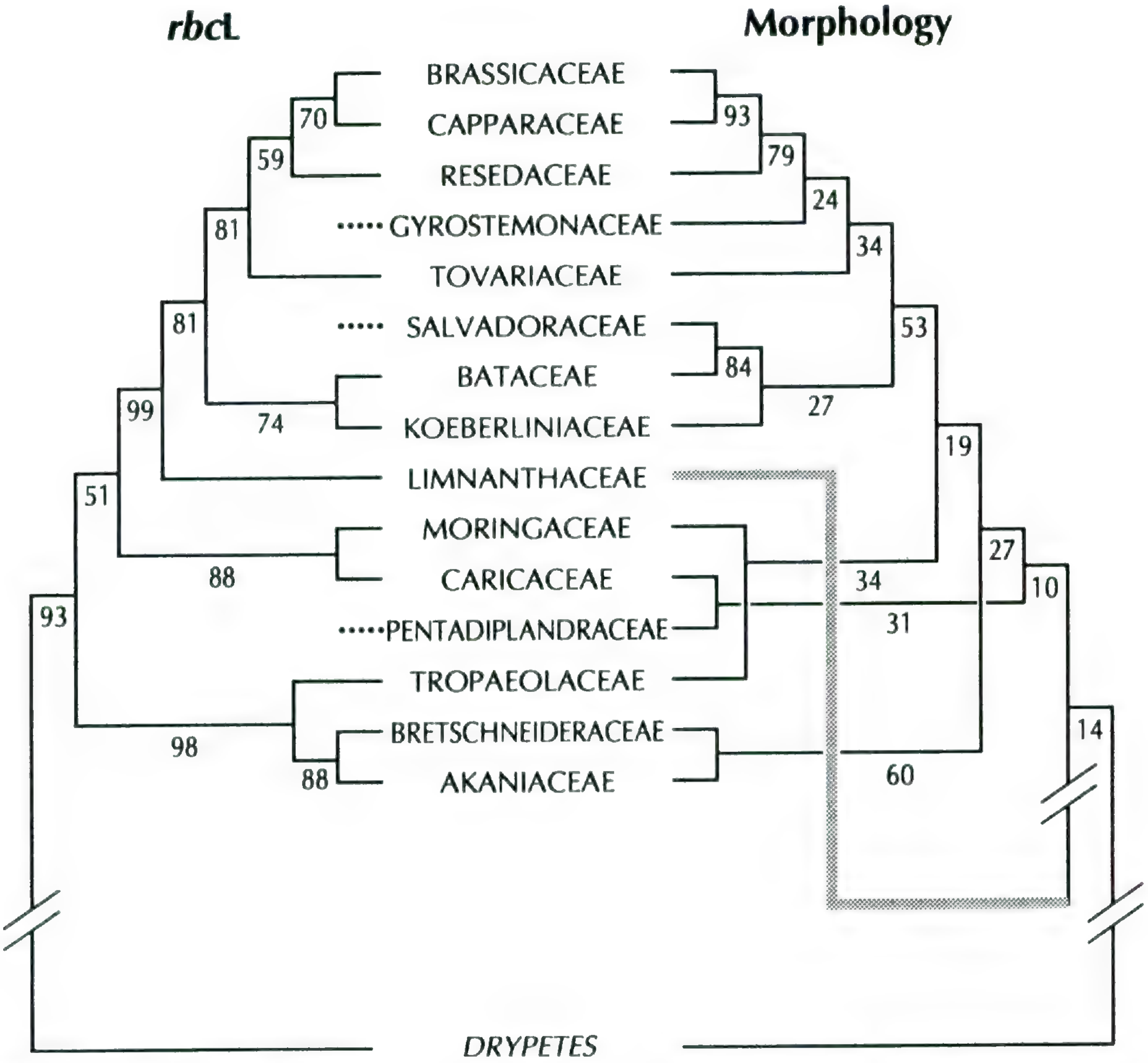


FIGURE 2. Comparison of the most parsimonious tree derived from *rbc*L sequence data (Fig. 1) with that from a prior cladistic study of predominantly morphological characters for the mustard oil taxa (Rodman 1991b, fig. 2). *Akania* has been incorporated in the *rbc*L tree from study of Gadek et al. (1992); Gyrostemonaceae, *Pentadiplandra*, and Salvadoraceae have not been sequenced. Breaks in lines indicate presence of intervening nonglucosinolate taxa. Bootstrap values (percentage of 100 replicates) are indicated for each branch; for the morphology tree, the published data set (Rodman, 1991a) was run in PAUP-version 3.0s to obtain bootstrap values.

version 3.0s) indicates that the union of Balsaminaceae + Limnanthaceae is weak, with a value of 23%. That character evidence is now called into question, as indeed it had been earlier by workers troubled with ambiguous homologies in embryology (Dahlgren, 1975b) and floral morphology (Hofmann & Ludewig, 1985; see Link, 1992). When we force Limnanthaceae into its *rbc*L-based position (using the TOPOLOGY option of PAUP: Swofford, 1985) and run the predominantly morphological data set, we obtain a tree eight steps longer than the most parsimonious ones found originally (Rodman, 1991b). Reduced homoplasy in phytochemical features (e.g., erucic acid and glucosinolate biosynthesis) is countered by increased homoplasy for morphological and chromosomal characters. The complementary test, running the *rbc*L data with Limnanthaceae forced into its morphology-based position as sister group to *Impatiens* (Balsaminaceae), results in an increase of 34 nucleotide changes over the 1,604-step trees. For *rbc*L data, potentially confounding events besides experimental error include introgression, lineage sorting, and mistaken orthology (Rieseberg & Soltis, 1991; Doyle, 1992). We consider all of these unlikely in the present case because of the taxonomic depth involved and the effectively single-copy evolution of the chloroplast genome (Palmer et al., 1988). Additional molecular data (especially nuclear genes) and evaluation of the chromosomal, morphological, and palynological homologies should reconcile the matter. At present we favor the *rbc*L

result because of the strength of its internal support compared to the weaker case in the morphology-based tree.

Character support for a major glucosinolate lineage had been judged weak in the prior cladistic study (Rodman, 1991b, table 1). That clade encompassed all the mustard oil taxa (plus *Koeberlinia*) except *Drypetes*, linked with Euphorbiaceae, and Limnanthaceae, linked with Balsaminaceae (Fig. 2). Only four homoplastic transformations were found to distinguish the stem lineage of this large mustard oil assemblage (presence of phenylalanine-derived glucosinolates, loss of anthocyanins, loss of methylated flavonols, and presence of myrosin guard cells). Bootstrap analysis reveals very weak support from the morphology data set, only 10% compared to 93% in the *rbc*L data. The sequence data thus provide independent and robust corroboration of a major mustard oil lineage. The results invite further scrutiny of the character homologies discussed by Rodman (1991a), particularly the anatomical and embryological features noted by Dahlgren (1975b).

In combination, the molecular and morphological results for the mustard oil taxa strongly support Dahlgren's (1975a, 1977) early classification of a greatly expanded Capparales. The inclusion of *Akania* (Gadek et al., 1992) and *Bretschneidera*, of *Batis* (an exoneration of Pulle's iconoclastic opinion: Eckardt, 1959), and of *Tropaeolum* departs radically from traditional taxonomic schemes and provides further evidence that Cronquist's (1981, 1988) subclasses Dilleniidae and Rosidae are not natural groups. Our results further suggest that Caricaceae and Limnanthaceae join the major glucosinolate clade. That would leave but a single outlying glucosinolate taxon. A distant *Drypetes*, phylogenetically linked near Euphorbiaceae, may thus constitute a remarkable example of molecular convergence. Both myrosin cells and glucosinolates of several biosynthetic types co-occur in *Drypetes*, as they do throughout the major mustard oil clade (*Koeberlinia* provides the single, fascinating exception). This conjoint anatomical-biochemical system remains an evolutionary mystery, albeit a mystery now limited to two branches of the angiosperm tree.

The deeply embedded position of *Koeberlinia* well within the major glucosinolate lineage (Fig. 1) further reinforces the idea (Rodman, 1981, 1991a, b) that it alone among members of this clade has lost or repressed the biochemical capacity to synthesize glucosinolates. Consistent with this interpretation, *Koeberlinia* has been reported to possess myrosin cells (Gibson, 1979).

The *rbc*L phylogeny creates novel linkages at the base of the major mustard oil clade, affiliations with little support in traditional taxonomic treatments of these plants. Linkages among these same taxa differ in the morphology-based tree, but bootstrap values are weaker (Fig. 2) and character support was judged weak as well (Rodman, 1991b, table 1). Caricaceae, for example, paired with the unsequenced *Pentadiplandra*, are basal in the morphology tree but with a bootstrap value of only 31%, whereas *Carica* and *Moringa* unite in the *rbc*L tree with robust support from bootstrap and decay analyses (Fig. 1B). We note, moreover, that our unpublished restriction-enzyme maps of chloroplast DNA demonstrate remarkable phenetic similarity between *Carica* and *Moringa*, especially in the conservative inverted-repeat region of the molecule. *Akania* (Gadek et al., 1992) and *Bretschneidera*, traditionally allied with Sapindales, are collateral with *Tropaeolum* in a strongly supported branch at the base of the major glucosinolate clade in our *rbc*L tree; hence, they are cladistically close to malvalean and sapindalean sister groups. Several phytochemists (see Kjaer, 1973) have proposed a biosynthetic linkage between the sulfur containing glucosinolates and cyanogenic glycosides; the widespread occurrence of cyanogens in Sapindales (Saupe, 1981) and of sulfated flavonoids in Malvales (Young, 1981) may prove more than coincidental. Likewise, the report of *Akania*, a genus currently restricted to Australia, in the Paleocene flora of Patagonia (Gandolfo et al., 1988) reduces the implausibility of a cladistic relationship with Andean Tropaeolaceae. Certainly these taxa are dissimilar in habit (Rodman, 1991a), but they may come to be seen as phenetically distant remnants of an early diversification of glucosinolate lineages. Sequence data from Gyrostemonaceae, *Pentadiplandra*, and Salvadoraceae are needed to complete the survey of all glucosinolate taxa, to resolve linkages among members of the major mustard oil clade, and to evaluate the double-origin hypothesis for glucosinolate biosynthesis proposed here.

Although much has been written about possible conflicts between molecular and morphological data in the study of phylogeny (Sytsma & Smith, 1988; Sytsma, 1990), this important theoretical problem is often obscured by a poor choice of examples employing incommensurable methodologies (e.g., Vickery & Wullstein, 1987; see Donoghue & Sanderson, 1992). Often, intuitively assessed morphological findings are compared to taxometrically analyzed molecular data, usually to the detriment of the former. In the current study, in which we have applied similar cladistic methods to both molecular

and morphological data, the results prove congruent in many areas of the topology and complementary in the strength they bring to particular lineages (Fig. 2). The morphological data provide stronger resolution of some terminal groups (e.g., within core Capparales) whereas *rbc*L data provide stronger resolution of relationships among basal glucosinolate clades, as judged by comparison of bootstrap values. In general, the strength of a data set of either type will depend on the number of robust characters that can be brought to bear at a particular taxonomic level. A major benefit of gene sequence data lies in the relative ease with which homology determinations can be made for numerous characters, compared to morphological data. It is for this reason that we favor the position of Limnanthaceae in the *rbc*L tree rather than the morphology-based result.

Finally, the results provide a commentary on the third assumption underlying our analysis: one or two samples can represent large families in *rbc*L phylogenies. Sequences for *Floerkea* and *Limnanthes* would seem reassuring in this context; published comparisons of several congeneric and confamilial taxa are similarly reassuring (Doebley et al., 1990; Hudson et al., 1990). But these results only beg the question: Is the family being represented a natural unit in the first place? The "Capparaceae" prove instructive. *Tovaria*, often treated as a subfamily of capers (Thorne, 1981, 1992), proves to be basal to a clade in which *Brassica* and *Reseda* are nested whether molecules or morphologies are studied. The nonglucosinolate *Koeberlinia*, often treated with capers as a subfamily also (Thorne, 1981, 1992), affiliates with *Batis* and Salvadoraceae (Rodman, 1991b), and *rbc*L data place it with *Batis*. *Cleome* links with *Brassica*, and these affiliate with *Capparis*, suggesting paraphyly for the Capparaceae even when pared of Koeberliniaceae and Tovariaceae. A more general message emerges. Whether one or few samples prove representative in *rbc*L surveys is contingent upon the monophyly of the terminal taxa. For many angiosperm families that cannot be taken for granted (Hershkovitz, 1989; Rodman, 1990; Soltis et al., 1990; Cantino, 1992; Donoghue et al., 1992).

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# A PARSIMONY ANALYSIS OF THE ASTERIDAE SENSU LATO BASED ON *rbc*L SEQUENCES[1]

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ABSTRACT

A parsimony analysis of 156 representative sequences of the Asteridae sensu lato and 28 outgroup sequences was conducted using a two-tiered approach. First, an analysis of the entire group, including 105 sequences, examined relationships among major lineages within the Asteridae s.l.; subsequently, several clades within the larger group were examined individually in greater detail by including more sequences for the group in question. The search strategy was designed to discover multiple islands of equal parsimony using the heuristic search routine in PAUP. In the broad search and in each more detailed search of subclades, multiple islands were found that imply substantially different relationships. The results suggest a monophyletic Asteridae s.l., comprising the Ericales, Primulales, Ebenales and relatives of the Dilleniidae sensu Cronquist; Cornales, Apiales, and Hydrangeaceae of the Rosidae sensu Cronquist; and the conventionally circumscribed Asteridae. Within the Asteridae s.l., 11 groups were congruent between islands and are designated as follows: (1) Cornales, (2) ericalean clade, (3) *Garrya* clade, (4) *Ilex* clade, (5) Apiales, (6) Dipsacales, (7) Asterales s.l., (8) Gentianales, (9) Solanales, (10) Boraginales, and (11) Lamiales s.l. The only grouping between the level of these 11 clades and the whole Asteridae s.l. that is congruent between islands is the clade consisting of the Gentianales, Solanales, Boraginales, and Lamiales s.l., i.e., the Lamiidae of Takhtajan.

Most recent constructs of the subclass Asteridae (e.g., Cronquist, 1981; Takhtajan, 1987) represent reduced groups of the former Gamopetalae (de Candolle, 1813), which was characterized primarily by fused corollas (see Wagenitz, 1977, 1992, for a more complete review of the development of ideas about the Asteridae). A series of traits interferes with the usefulness of the simple dichotomy of fused versus free petals in defining major groups in the "higher" dicots (i.e., the tricolpate clade of Donoghue & Doyle, 1989), including number of stamen whorls and their position relative to corolla lobes (Dahlgren, 1983); embryological characters, such as one versus two integuments and the crassi- versus tenuinucellar condition in the ovule (Dahlgren, 1975); and, more recently, the distribution of secondary chemicals, particularly iridoids (Jensen, 1992). A "group" defined on the basis of any one of these traits will be incongruent with a "group" defined on the basis of any other (Wagenitz, 1977).

Conventional approaches to classification often proceed by *defining* groups on the basis of one or a few clearly defined traits, with additional traits used to refine groups and establish subgroups. In contrast, phylogenetic classification relies on the identification of derived traits to *discover* groups that are hypothesized to be monophyletic. Molecular approaches to systematics have become popular, in part, because they usually are well suited to phylogenetic analysis. Another reason for the popularity of molecular systematics is that phylogenetic hypotheses generated by molecular data generally are independent of the morphological traits in which many evolutionary biologists are interested.

With the combination of phylogenetic systematics and molecular methods, plant systematics has entered a new period of discovery. With respect to the Asteridae, we are not simply testing hypotheses set forth by previous workers (e.g., Cronquist, 1981; Dahlgren, 1980; Takhtajan, 1987; Thorne, 1992); instead we are discovering groups, and those groups may or may not reflect traditional classifications. However, we are indebted to pre-

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vious workers for providing a framework for sampling in molecular studies. It is fortunate that there has been disagreement among conventional angiosperm phylogeneticists, or else our sampling may have been biased. The possibility of biased sampling combined with the limited body of data yet produced by molecular systematists means that interpretations should be made with caution. Suggestions made today (e.g., based on *rbc*L sequences) may be viewed in the not-too-distant future as we view those of 19th-century botanists. The results reported here fall into three classes: (1) results congruent with traditional classifications, (2) results resolving relationships of taxa ambiguously placed in traditional classifications, and (3) novel results wherein the sequence data are in apparent conflict with conventional data. To be treated properly, these novel results should be considered as starting points for further studies, in which both morphological *and* molecular data are re-examined and supplemented with additional data.

Recent efforts at discovering a monophyletic Asteridae (Downie & Palmer, 1992; Hufford, 1992; Olmstead et al., 1992) identified a large clade containing the Asteridae sensu stricto and several elements generally excluded from traditional circumscriptions of the group, including the Apiales, Ericaceae, Fouquieriaceae, Cornaceae, Hydrangeaceae, Loasaceae, and Columelliaceae. Olmstead et al. (1992) referred to this clade as the Asteridae sensu lato and identified four major lineages comprising the group, with relationships unresolved among them. The four lineages were the (1) ericalean clade (Ericaceae, Polemoniaceae, Fouquieriaceae), (2) cornalean clade (Cornaceae, Hydrangeaceae), (3) Asteridae sensu Takhtajan (1987) plus Apiales (Asterales, Campanulales, Goodeniales, Menyanthaceae, Dipsacales, Apiales), and (4) Lamiidae sensu Takhtajan (1987) (Gentianales, Solanales, Boraginales, Lamiales, and Scrophulariales). Restriction site analysis of the cpDNA inverted repeat region (Downie & Palmer, 1992) for the Asteridae s.s. and putative relatives concurred in finding a cornalean group, a group consisting of Polemoniaceae and Fouquieriaceae (Ericaceae was not sampled), and the Lamiidae (Takhtajan, 1987). Hufford (1992) identified a large Corniflorae asterid group including a cornalean clade, an ericalean clade (excluding Polemoniaceae), and a conventional asterid clade (including Pittosporaceae and Columelliaceae).

Current work presented here and in accompanying papers represents another step toward discovering the best circumscription of the Asteridae sensu lato and groups within it. This series of papers is a fitting follow-up to the "Phylogeny of Asteridae" symposium proceedings published in this journal (Ann. Missouri Bot. Gard. 79(2), 1992), containing as it does papers on groups belonging to the Asteridae s.s. (Michaels et al., 1993) and papers on groups now included in the Asteridae s.l. (Xiang et al., 1993; Morgan & Soltis, 1993; Kron & Chase, 1993), in addition to this one on the Asteridae s.l.

A detailed study examining which sequences belong in or out of a group as large as the Asteridae s.l. is a formidable task. Olmstead et al. (1992) established a series of goals for their molecular studies of the Asteridae and addressed the first two: (1) to evaluate the monophyly of the Asteridae and (2) to identify major lineages within the Asteridae. This study addresses the next two goals: (3) to circumscribe ordinal-level groups through greater sampling and (4) to determine relationships among them. We anticipate that this will bring us one step closer to the final goals of a revised classification of the Asteridae and of a better understanding of evolutionary patterns and trends within the group. By focusing on the Asteridae s.l., we examine in much greater detail the *rbc*L data for taxa suggested to belong to the group than is possible in the analyses of Chase et al. (1993, this issue). The coarse nature of the broad-scope analyses of Chase et al. (1993) weakens their utility as rigorous hypotheses of relationship, but they do serve a useful purpose by suggesting sets of taxa that merit inclusion in more detailed analyses such as this one.

The analysis and interpretation of large data sets are complicated by the probable existence of multiple islands of trees representing equally or nearly equally parsimonious solutions (Maddison, 1991). A single parsimony analysis, even one using a detailed search strategy, can identify only one island. Identifying and presenting separate islands of equal parsimony, or even within one or two steps of the shortest trees (especially when these trees may contain 2,000–4,000 steps), provide valuable insight into possible patterns of relationship and are essential when revised classifications or interpretations of character evolution are to be based on the outcome of a phylogenetic analysis. An inadequate analysis, in which a search for multiple islands is not carried out, may produce exaggerated resolution, lead to misleading conclusions, and deter potential lines of further research.

## Materials and Methods

The sequences included in the analyses reported here have been published previously (e.g., Olm-

stead et al., 1992), are from various researchers and included in the seed plant analysis of Chase et al. (1993), or are reported for the first time here. All sequences and their sources are listed in the Appendix at the end of this issue. Some of the sequences were obtained as described previously (Olmstead et al., 1992). The remaining sequences were determined by first PCR-amplifying the entire gene from a total DNA extract by use of primers described in Olmstead et al. (1992). Single-stranded DNA for dideoxy sequencing was then obtained by a second round of PCR using 0.01 μl of the original PCR product as template and a 1:100 primer ratio with the excess primer in the same concentration as in the initial PCR run.

Nucleotide positions 27–1428 were included in the cladistic analyses, but the actual number of nucleotides varied among species depending on whether sequences were complete for this region (see Appendix at end of issue). Positions 1–26 represent the PCR primer sequence for most sequences, and after position 1428 sequence alignment becomes problematic.

Several subsets of the entire data set were compiled to examine the entire Asteridae s.l. generally and several internal clades specifically, as well as to examine the question of sister group to the Asteridae s.l. In all cases, care was taken to include a number of outgroups, which were selected following examination of the results of an analysis of 475 *rbc*L sequences ("Search I" of Chase et al., 1993).

Parsimony analyses were conducted using PAUP 3.0s (Swofford, 1992) on a Mac IIfx. All analyses were conducted with equal weights assigned to all changes. The general search strategy proceeded as follows (variations are discussed in Results). First, two or more replicates of 200–1,000 searches each were carried out using a random-order, sequential entry with NNI branch swapping (nearest neighbor interchanges), STEEPEST DESCENT on, and with the MULPARS option off. The goal of this phase of the search was to increase the chance of locating the island or islands containing the shortest trees by finding a reasonably short tree to initiate a more detailed search. The shortest tree or trees from each replicate was entered separately as the starting point for the second phase search for all equal-length trees reachable from that starting point. The second phase of the search proceeded by using TBR swapping (tree bisection-reconnection) with MULPARS on. Searches on each individual data set, except for the one examining sister group relationships to the Asteridae s.l., were pursued until two or more islands of trees were discovered.

## Results

### Analysis of Asteridae s.l.

An analysis of 184 *rbc*L sequences is reported here, including 156 representatives of the Asteridae s.l. and 28 outgroup sequences. To examine the entire Asteridae s.l., a set of 105 sequences was compiled. To reduce the complexity of the data set while maintaining the best-possible distribution of taxa, several well-supported families with multiple representatives (e.g., Asteraceae, Acanthaceae, Cornaceae) were thinned from the number of representatives in the analyses of Chase et al. (1993, this issue). Choice of outgroup sequences was guided by the results of "Search I" of Chase et al. (1993). Five sequences (*Gunnera*, *Paeonia*, *Phoradendron*, *Schoepfia*, *Osyris*) comprising a clade identified as the sister group to the Asteridae s.l. in that search were included. Six progressively more remote outgroups, *Heuchera* and *Cercidiphyllum* ("rosid IV" clade of Chase et al., 1993), *Dianthus* ("rosid III"), *Tetracentron* ("hamamelid II"), *Platanus* ("hamamelid I"), and *Caltha* ("ranunculid"), were also included. All outgroups are "higher" dicots (sensu Donoghue & Doyle 1989), to minimize the problem of long outgroup branches (Swofford & Olsen, 1990), and fall outside the broadest possible circumscription of the Asteridae s.l. based on traditional or molecular evidence. Most of the outgroups belong to the closest sister groups (rosids and caryophyllids) to the Asteridae s.l. as identified by the subsequent and more complete "Search II" of Chase et al. (1993).

The search for the shortest trees connecting 105 sequences of the Asteridae s.l. and outgroups represents a major computational effort and resulted in the discovery of three islands of trees of equal parsimony. Considering the amount of time and effort expended in acquiring a data set of this size, the data deserve the substantial effort dedicated to their analysis. A more detailed description of the approach used will be described for this data set than for subsequent searches. As with any search where the number of taxa is above the limit of a branch-and-bound search algorithm (i.e., ca. 20 taxa), there is no way to guarantee finding the shortest tree or trees.

The search was initiated by performing 200 random-order-entry replicate searches using NNI swapping with MULPARS off (this search required approximately 5 hours and found one tree of length 3,609). The resulting tree was then used as a start for a search using TBR swapping with MULPARS off (26 min., length = 3,605), which was used, in turn, as the start for a search using NNI with

MULPARS on (2 hours, 432 trees of length 3,601). These trees were then used as the starting point for a search using TBR with MULPARS on. This search was terminated prematurely without swapping on all trees when the computer RAM buffer reached a limit of 4,600 trees (approximately 4 days, length = 3,600). An attempt to find shorter trees was then made by dividing the tree file into many smaller files containing subsets of the 4,600 trees. TBR swapping was initiated on several Mac II computers simultaneously with MAXTREES set to the number of trees in each subset plus one. This strategy enables TBR swapping to proceed on all 4,600 trees saved, but will not save any more trees. The search for shorter trees from the 4,600 trees of length 3,600 lasted several days with as many as eight computers operating simultaneously. Two separate trees of length 3,600 each led to the same island (Maddison, 1991) of 102 equal-length trees (length = 3,597).

The resulting strict consensus tree (Fig. 1A) for island-102 (terminology of Maddison, 1991) shows a basal split in the Asteridae s.l. with one branch consisting of the Lamiidae and the small *Garrya* clade and the other consisting of the ericalean clade, the Cornales (including the Hydrangeaceae), Apiales, Dipsacales, Asterales s.l., and the small *Ilex* clade. In addition to the basal split into two major lineages, this tree differs from the results of Chase et al. (1993) in showing the Cornales as a more derived branch than the ericalean clade.

While this search was in progress, a second search was initiated on the same set of 105 sequences by performing 1,000 random-order-entry replicate searches using NNI swapping with MULPARS off (26 hours, one tree, length = 3,605). This tree was then input directly into a search using TBR swapping with MULPARS on. This search required approximately 10–12 weeks computer time and resulted in the discovery of a second island of length 3,597 containing 2,784 trees (Figs. 1B, 2). During this search >6,300 trees were found at one step longer, of which >3,500 were swapped before a shorter tree was found. The topology of the strict consensus tree (Fig. 1B) for island-2,784 is dramatically different from that derived from island-102 with respect to the relationships among the primary groups identified within the Asteridae s.l. These results unite the Lamiidae with the Asterales s.l., thus forming a clade equivalent to the Asteridae of Cronquist except for the exclusion of the Dipsacales. The Dipsacales and Apiales together are sister group to the above-mentioned clade, with the small *Ilex* and *Garrya* clades each forming progressively more basal branches, and the Cornales and ericalean clade producing a basal trichotomy.

After the first two islands were discovered using the search strategy outlined above, another approach to finding initial trees, possibly representing separate islands, was tried (suggested by D. Maddison, pers. comm.). One hundred replicate random-order-entry searches were conducted using TBR swapping with MULPARS on, but with the option to save no more than two trees greater than, or equal to, length "X," where "X" is a number small enough to be certain to be shorter than the shortest tree found. This approach enables each random start to be searched much more completely than the approach outlined above. One replicate yielded two trees of length 3,597 and which were topologically distinct from any tree belonging to island-102 or island-2,784. A search for all most parsimonious trees yielded 5,568 trees at that length. The initial search required 11 days and the search for all parsimonious trees in the island required an additional seven weeks to complete. This island contains exactly twice as many trees as island-2,784 and can be accounted for by one additional polytomy (within the Gentianales). Topologically, this island is identical with island-2,784, except that the Boraginales are united with the Gentianales instead of with the Solanales and the relationships among the five sequences representing the Gentianales are different (hence this island is not illustrated). Figure 3 shows the strict consensus of all trees discovered in the three islands.

Another analysis was performed to explore more fully the putative sister group to the Asteridae s.l. "Search I" of Chase et al. (1993, this issue) identified the clade mentioned above as sister group, whereas their "Search II" (Chase et al., 1993) identified a small clade of two sequences (*Dillenia* and *Vitis*) as sister group to the Asteridae s.l. For this analysis, 40 sequences of the Asteridae s.l. were removed and 17 additional dicot sequences were included, giving a total of 82 sequences. This analysis found 30 equal-length trees of length 3,322 (Fig. 4). This search was initiated with 300 random-order-entry replicate searches and was not replicated to find alternate islands, but the search strategy was equivalent to that used to find one of the shortest islands in other analyses reported here. This result is congruent with that based on the previous analysis in suggesting that the Santalales, *Paeonia*, and *Gunnera* do not belong together or with the Asteridae s.l. and more likely belong in the large clade identified as Rosidae s.l. in the analyses of Chase et al. (1993). The results do not place the *Dillenia* and *Vitis* sequences as sister

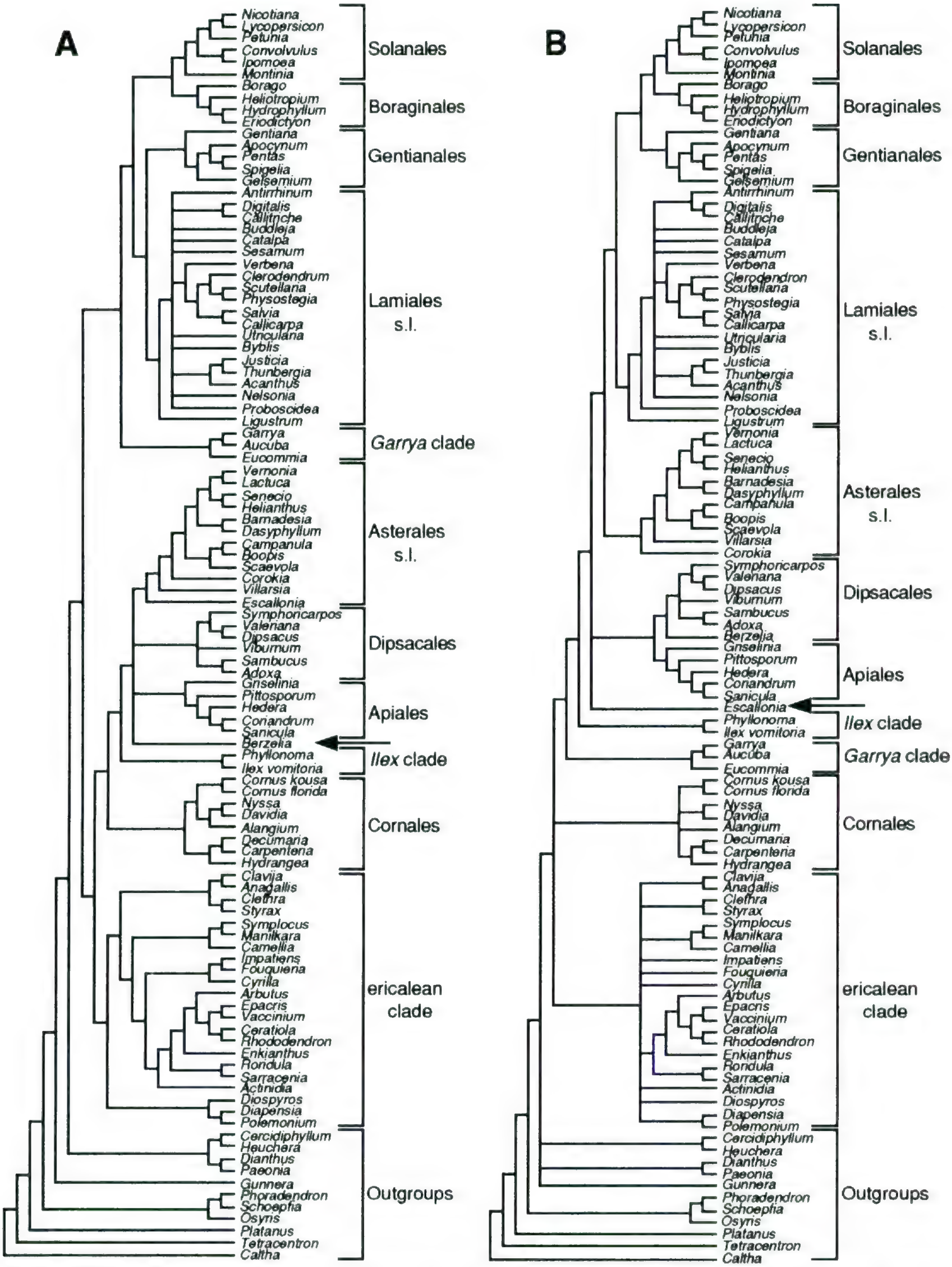


FIGURE 1. Strict consensus trees for two islands of equal parsimony in the Asteridae s.l. (105 *rbc*L sequences, including 11 outgroups; length = 3,597; C.I. = 0.25; R.I. = 0.51).—A. Island-102. Strict consensus of 102 trees.—B. Island-2,784. Strict consensus of 2,784 trees. Eleven clades that are congruent between the two islands and island-5,568 (not shown) are identified. Arrows identify sequences that resolve to a specific clade in one island, but not in the other.

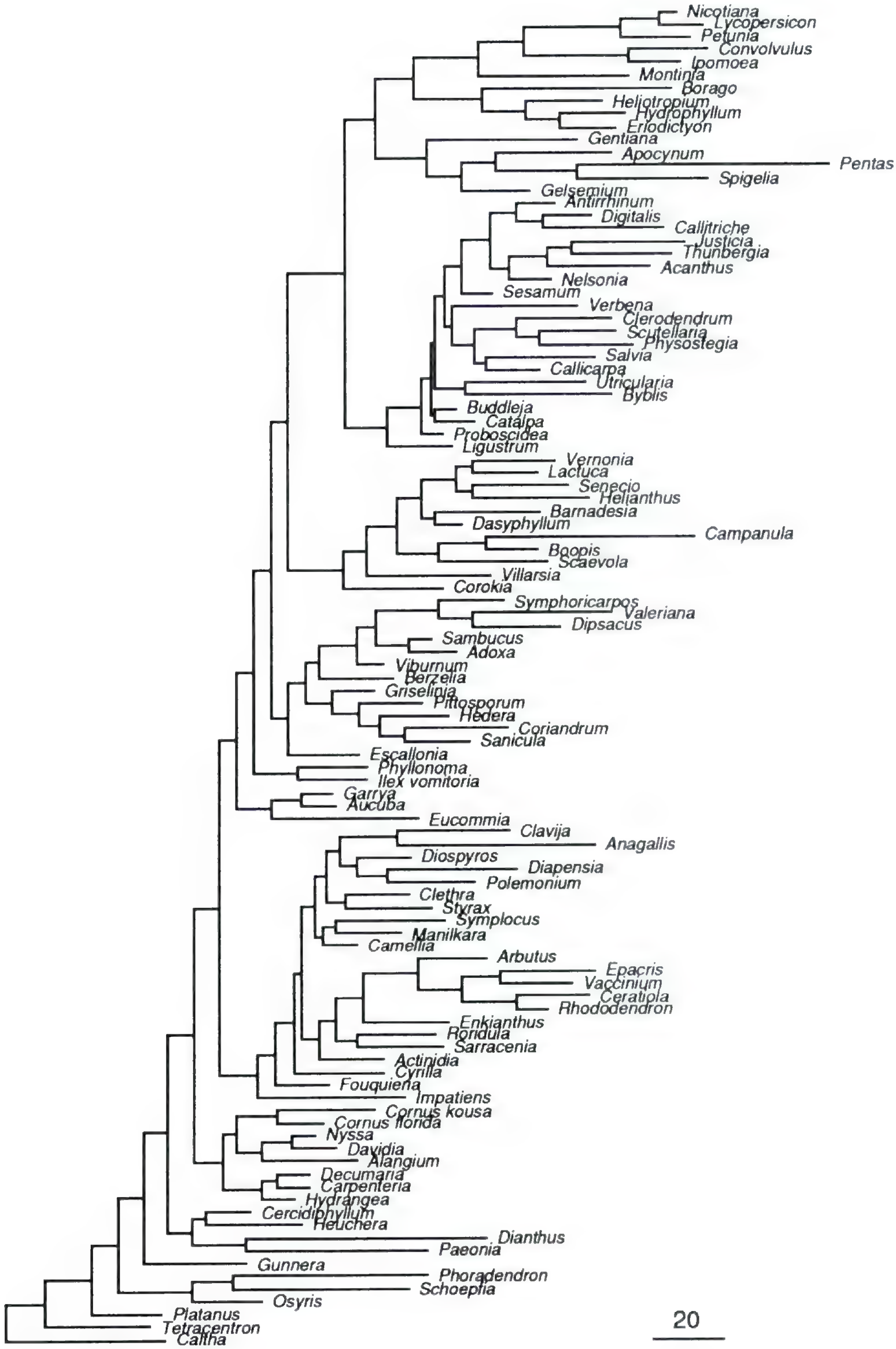


FIGURE 2. Majority rule consensus tree of island-2,784 selected as representative tree to illustrate branch lengths (ACCTRANS optimization). Particularly long branches are evident in *Pentas* (Rubiaceae) and *Campanula* (Campanulaceae); see discussion concerning incongruent results in different analyses containing these sequences (e.g., *Pentas* in Figs. 3 and 5). Note scale bar equal to 20 inferred nucleotide substitutions.

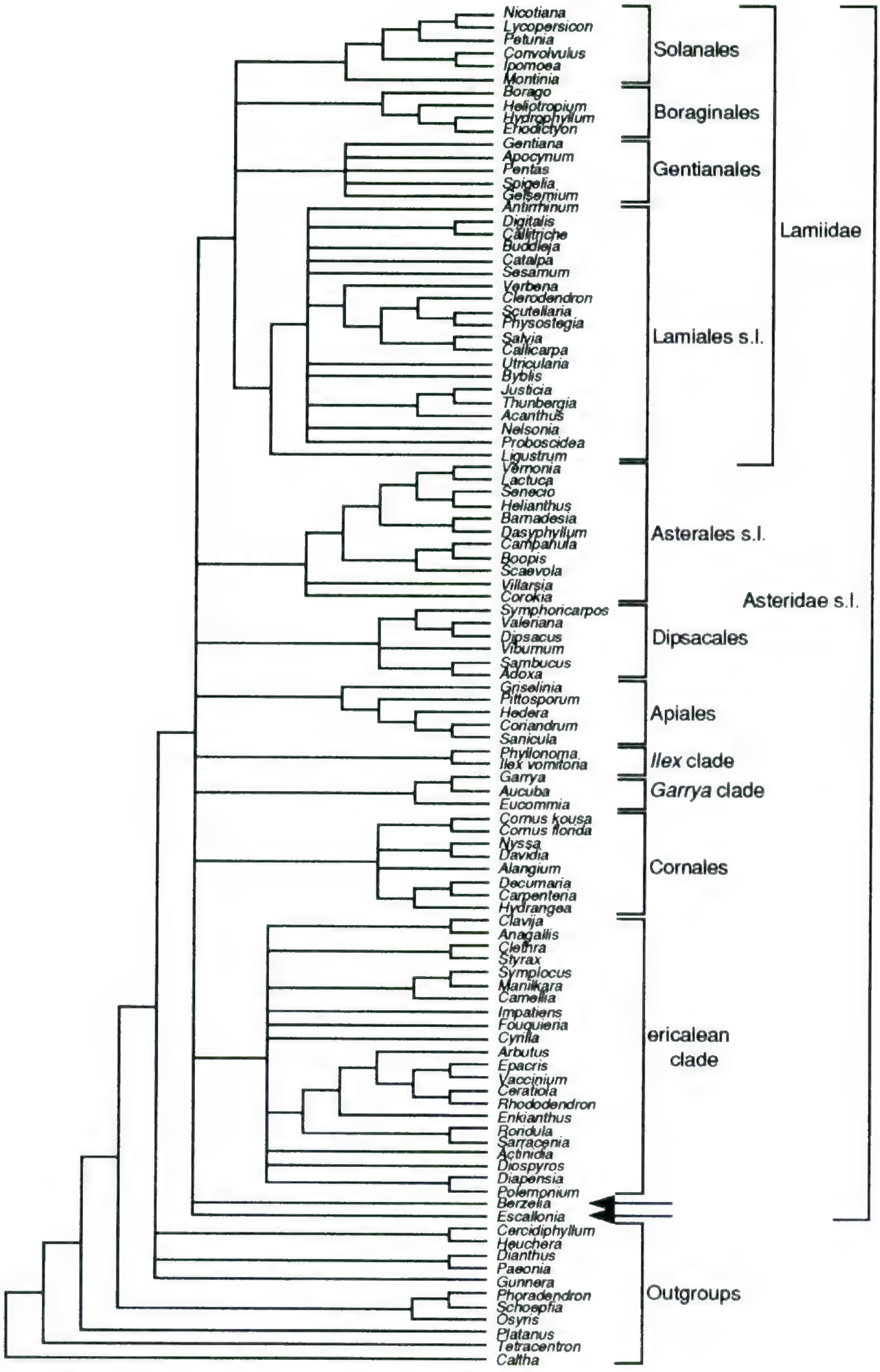


FIGURE 3. Strict consensus tree of 8,454 equal-length trees based on *rbc*L sequences. Trees from three islands (island-102, island-2,784, and island-5,568) are combined. Eleven terminal clades that are congruent among all three islands are identified. The Lamiidae sensu Takhtajan (1987) is the only group resolved between the level of the 11 congruent clades and the entire Asteridae s.l. *Berzelia* and *Escallonia* (indicated with arrows) are not resolved to any of the clades that are congruent between islands.

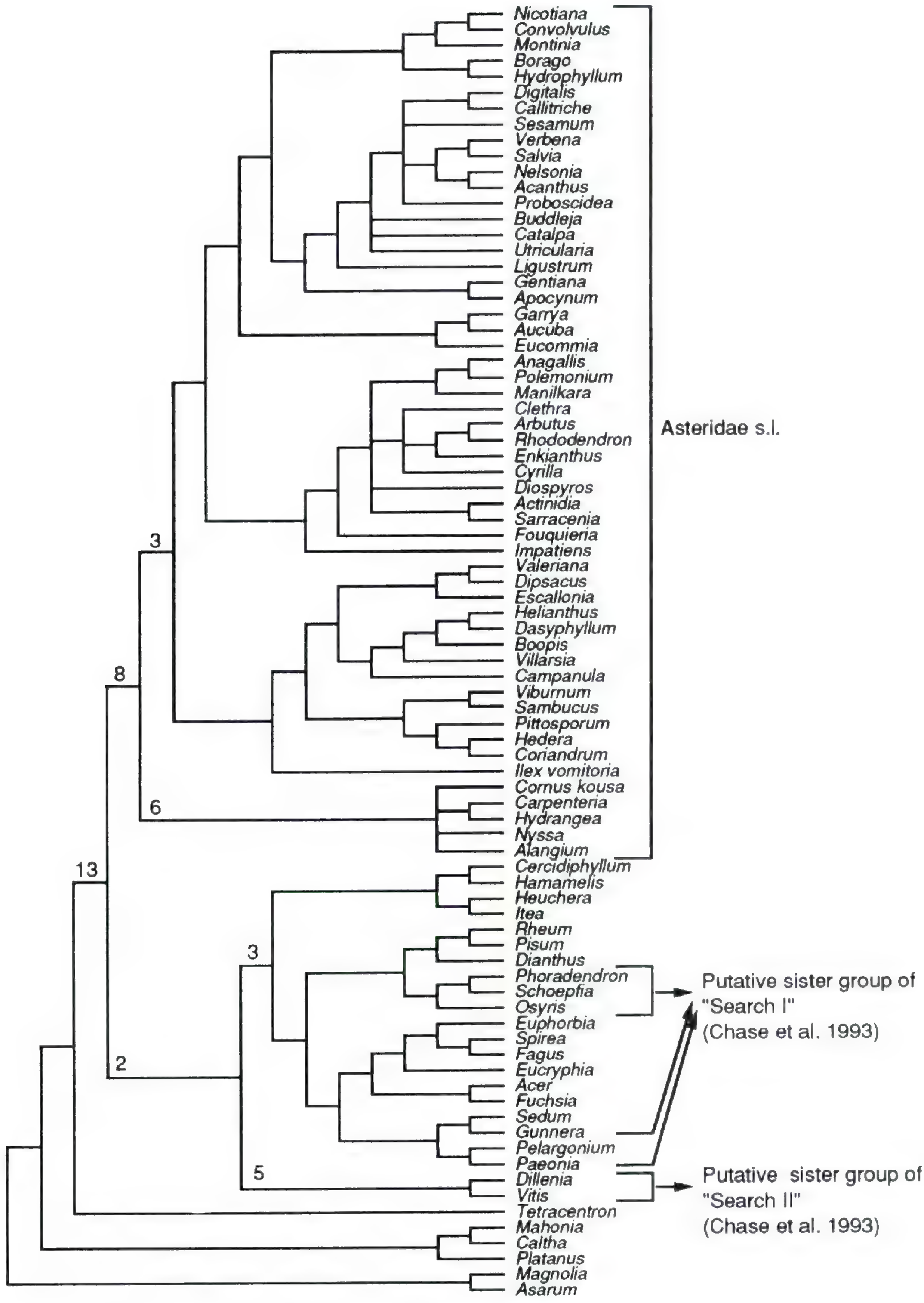


FIGURE 4. Strict consensus of 30 trees based on *rbc*L sequences resulting from the analysis designed to explore sister-group relationships to the Asteridae s.l. (length = 3,322, C.I. = 0.25, R.I. = 0.41). The sister group to the Asteridae s.l. indicated by this analysis is a large clade consisting of parts of the Rosidae and Dilleniidae sensu Cronquist (1981). Putative sister groups suggested by "Search I" and "Search II" of Chase et al. (1993) are indicated. Typical branch lengths in the vicinity of the node from which the Asteridae s.l. and their sister group diverge are indicated.

group to the Asteridae s.l. either. Instead, these sequences are placed at the base of the Rosidae s.l., suggesting that they represent a clade that diverged close to the divergence of the two larger clades. A search for multiple islands might find equal length trees congruent with the results of "Search II" of Chase et al. (1993) with respect to the placement of these two sequences.

ANALYSIS OF SUBCLADES

Detailed analyses were conducted on three subsets of the asterid *rbc*L data that were identified as clades by Olmstead et al. (1992) and in "Search I" of Chase et al. (1993). The primary purpose for the subclade analyses is to examine in detail more sequences within major clades than is possible in the more inclusive broad analysis of the Asteridae s.l. Thus, the subclade analyses are viewed in relationship to the Asteridae s.l. analysis as that analysis is to the seed plant analyses of Chase et al. (1993). Results from this nested hierarchical approach should be complementary; the local analyses better assess relationships within terminal clades and the broader analyses better assess relationships among those clades. Time considerations dictated that selection of these subsets of sequences precede the completion of "Search II" (Chase et al., 1993) and the search for multiple islands conducted on the 105-sequence Asteridae s.l. data set described above. The first subset analyzed is the Lamiidae sensu Takhtajan (1987). The second (hereafter referred to as the Asterales–Dipsacales–Apiales) contains the Asterales, Campanulales, Dipsacales, Apiales, and several taxa traditionally assigned to other orders in the Asteridae or Rosidae (sensu Cronquist, 1981). Both "Searches I & II" of Chase et al. (1993) identified a small clade containing *Garrya* (Garryaceae), *Aucuba* (Cornaceae), and *Eucommia* (Eucommiaceae) placed near the point of divergence of the two above-mentioned, larger clades. To examine the possible relationships of these three taxa, they were included in each analysis. The third clade examined in greater detail is one containing representatives of the Ericales, Ebenales, Primulales, and other taxa from the Rosidae, Dilleniidae, and Asteridae. The Cornales and Hydrangeaceae represent the only primary group within the Asteridae s.l. not included in a more detailed analysis here, because a detailed analysis of this group appears elsewhere (Xiang et al., 1993).

To examine the Lamiidae, a set of 72 sequences was compiled. This set included all of the sequences belonging to the group "Asteridae I" in "Search II" of Chase et al. (1993), except *Vahlia*, and included nine additional sequences from taxa traditionally assigned to the orders Gentianales (six) and Scrophulariales (three). Outgroup sequences included *Cornus* (Cornaceae), *Nyssa* (Nyssaceae), *Arbutus* (Ericaceae), *Polemonium* (Polemoniaceae), *Ilex* (Aquifoliaceae), *Escallonia* (Grossulariaceae), *Hedera* (Araliaceae), *Viburnum* (Caprifoliaceae), and *Dasyphyllum* (Asteraceae). The analysis of the Lamiidae data set (72 sequences) resulted in the discovery of four islands (although more may exist); two islands contain 135 (Fig. 5) and 1,350 trees (Fig. 6A), each of 2,189 steps, whereas the other two are one step longer (see below). Both islands identify as clades the Solanales (e.g., Solanaceae, Convolvulaceae, and *Montinia*), Boraginales (e.g., Boraginaceae, Hydrophyllaceae), Lamiales s.l. (e.g., Oleaceae, Bignoniaceae, Labiatae, Verbenaceae, Scrophulariaceae, Acanthaceae), and Gentianales (e.g., Rubiaceae, Gentianaceae, Apocynaceae, Loganiaceae), with a clade comprising the Solanales and Boraginales sister group to the others. The differences between the two islands fall entirely within the Lamiales s.l. clade, where several individual sequences or small groups of sequences occupy very different positions. Much resolution within the Lamiales s.l. is lost in the strict consensus of both islands combined (Fig. 6B). Both islands identify the *Garrya–Aucuba–Eucommia* clade as sister group to the Lamiidae. Two additional islands (not shown) containing 2,160 and 135 trees representing local optima were discovered at one step longer (2,190 steps). These trees are identical to the shorter islands with respect to the pattern of relationships among primary lineages within the Lamiidae, but differ in that the *Garrya* clade is not identified as their sister group.

To examine the Asterales–Dipsacales–Apiales, a set of 43 sequences was compiled. This set included all of the sequences belonging to the group "Asteridae II" in "Search II" of Chase et al. (1993), except that six representatives of the Asteraceae were included (rather than 14), and one additional sequence each of *Ilex* and of Apiaceae were added. *Garrya*, *Aucuba*, and *Eucommia* were included. Outgroup sequences included *Cornus*, *Nyssa*, *Arbutus*, *Polemonium*, *Nicotiana* (Solanaceae), *Gentiana* (Gentianaceae), and *Antirrhinum* (Scrophulariaceae). The analysis of this data set resulted in the discovery of two islands containing 80 (Fig. 7A) and 196 trees (Fig. 7B) each of 1,368 steps. The smaller island identifies a monophyletic Asterales–Dipsacales–Apiales, whereas the island of 196 trees (Fig. 7B) is unresolved with respect to these three orders and

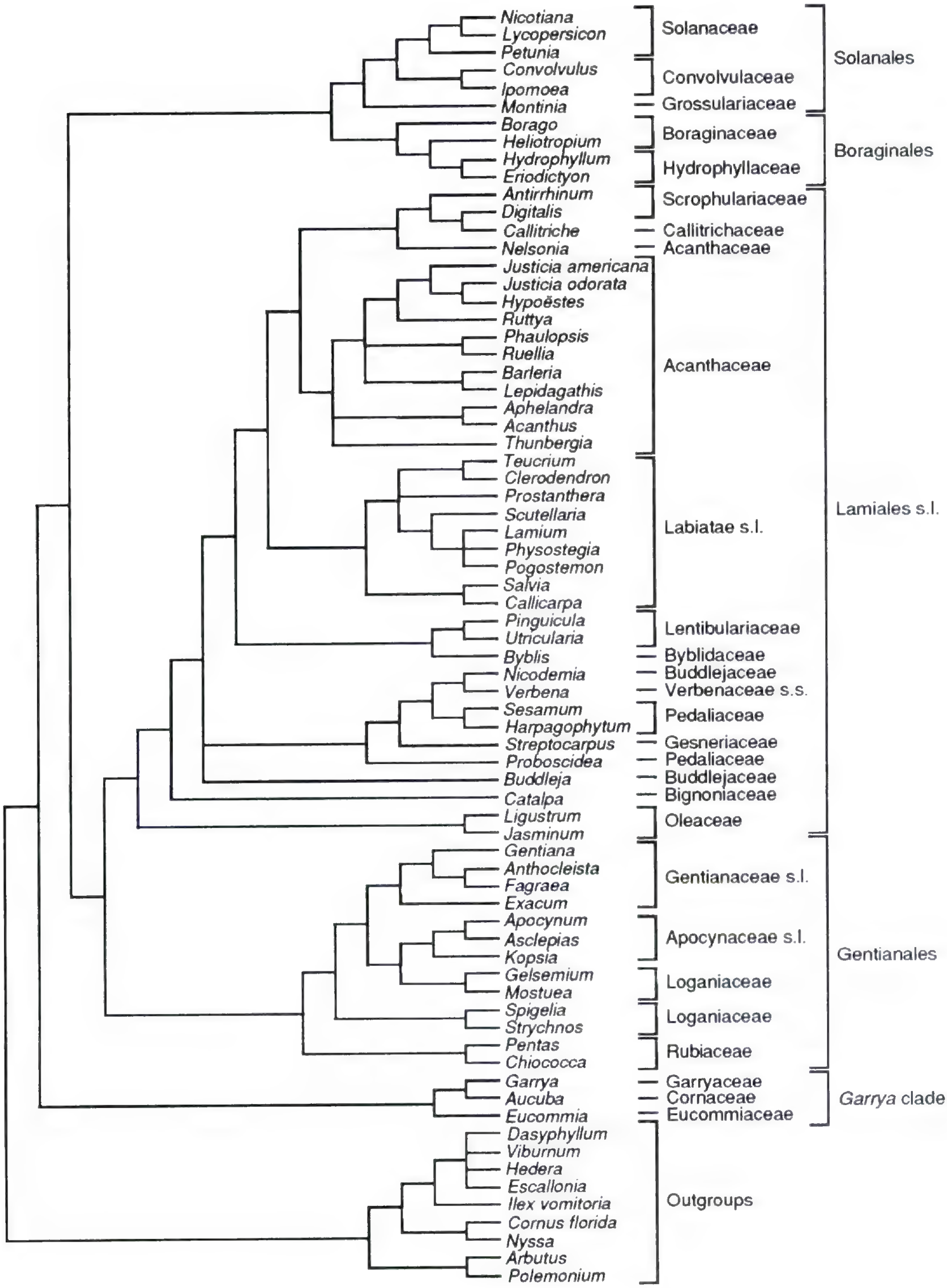


FIGURE 5. Lamiidae, island-135. Strict consensus of 135 trees based on *rbc*L sequences with increased taxon sampling in the Lamiidae (length = 2,189, C.I. = 0.31, R.I. = 0.57). Family designations follow Cronquist (1981), except for the Labiatae (Cantino et al., 1992), and do not imply necessarily that the entire family belongs where these representatives occur. Two additional islands each one step longer place the *Garrya* et al. clade among the other designated outgroups and not as sister group to the Lamiidae (not shown).

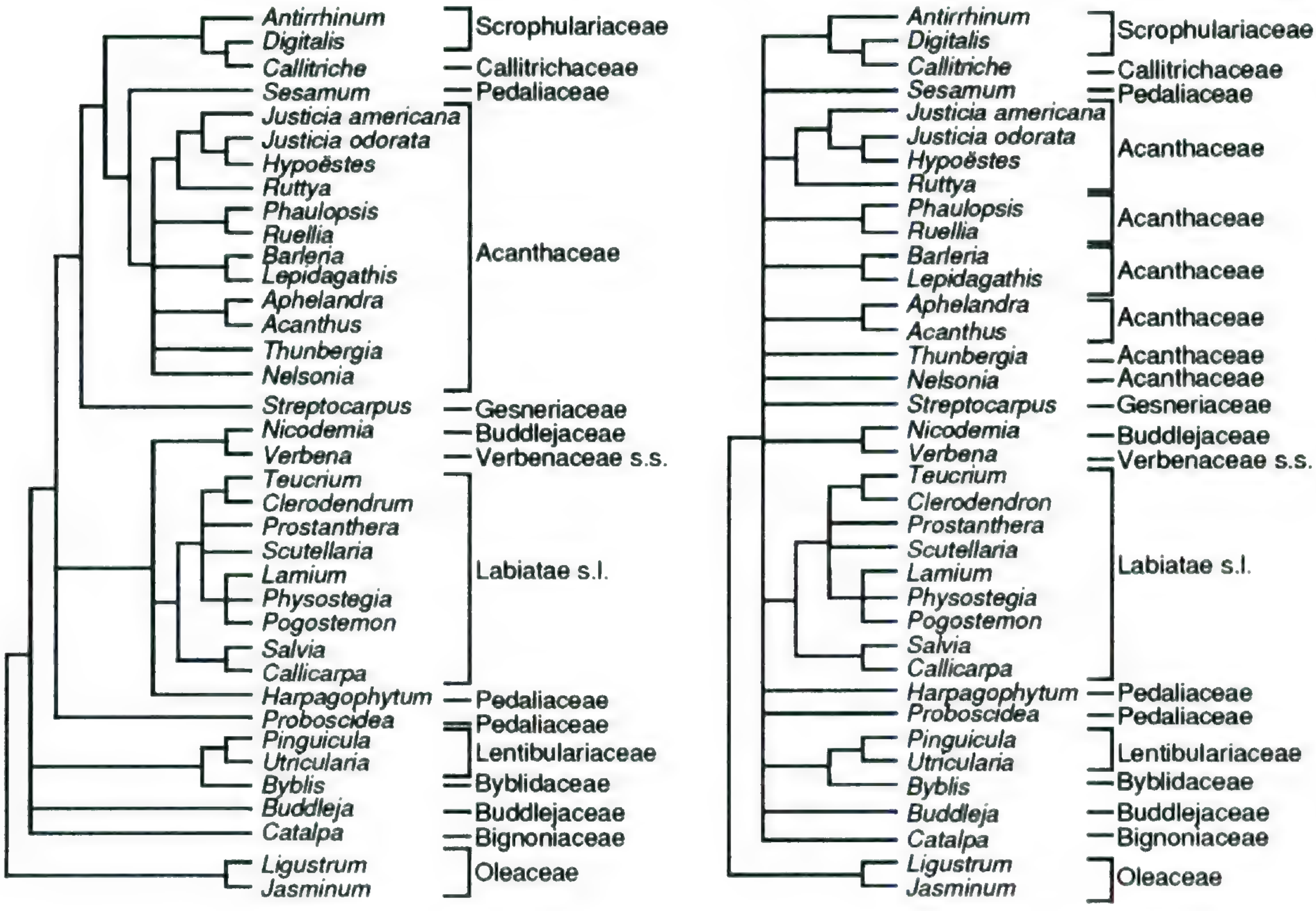


FIGURE 6. Strict consensus trees of the Lamiales s.l. based on *rbc*L sequences. These trees represent the portion of the Lamiidae analysis that is variable among islands; relationships among other members of the Lamiidae and outgroups are the same as in Figure 5.—A. Island-1,350. Strict consensus of 1,350 trees (length = 2,189, C.I. = 0.31, R.I. = 0.57).—B. Strict consensus of 1,485 equal-length trees from island-135 and island-1,350 combined. Family designations as in Figure 5.

several other groups (however, the Dipsacales and Apiales group with representatives of the Cornales in many trees). This is similar to the results of the Asteridae s.l. analysis, in which one island identifies this clade (Fig. 1A) and the other does not (Fig. 1B). Both islands identify the following clades: Dipsacales, Asterales s.l. (including Campanulales, Menyanthaceae, and *Corokia*), Apiales (including *Pittosporum* and *Griselinia*), and the group containing *Ilex*, *Phyllonoma*, and *Helwingia*.

To examine the ericalean clade, a set of 60 sequences was compiled, including all of the sequences belonging to the group "Asteridae III" in "Search II" of Chase et al. (1993) except *Heliamphora*. Eight additional sequences representing the Ericaceae were included (see Kron & Chase, 1993). Nineteen representatives of other clades in the Asteridae s.l. were included as outgroups. The analysis of this data set resulted in the discovery of two islands of trees, one containing 612 trees (Fig. 8B) of 1,889 steps and the other containing 357 trees (Fig. 8C) of 1,890 steps. Both islands identify a monophyletic Ericaceae s.l. (including the Epacridaceae, Empetraceae, and Pyrolaceae), in agreement with Kron & Chase (1993). All members of this clade belong to Cronquist's Dilleniidae, except *Impatiens*, *Roridula*, and *Polemonium* (see discussion below). The largest clade that is congruent between the two islands is the Ericaceae. The shorter island is congruent in most respects with the results of Kron & Chase (1993). The strict consensus tree of both islands combined indicates very little resolution outside the Ericaceae (Fig. 8A).

## DISCUSSION

The goals of a study of this nature (i.e., reconstructing the phylogeny of the Asteridae) are lofty, but accomplishing them is problematic. A major problem with analyzing this and any other large and complex systematic data set is assessing the

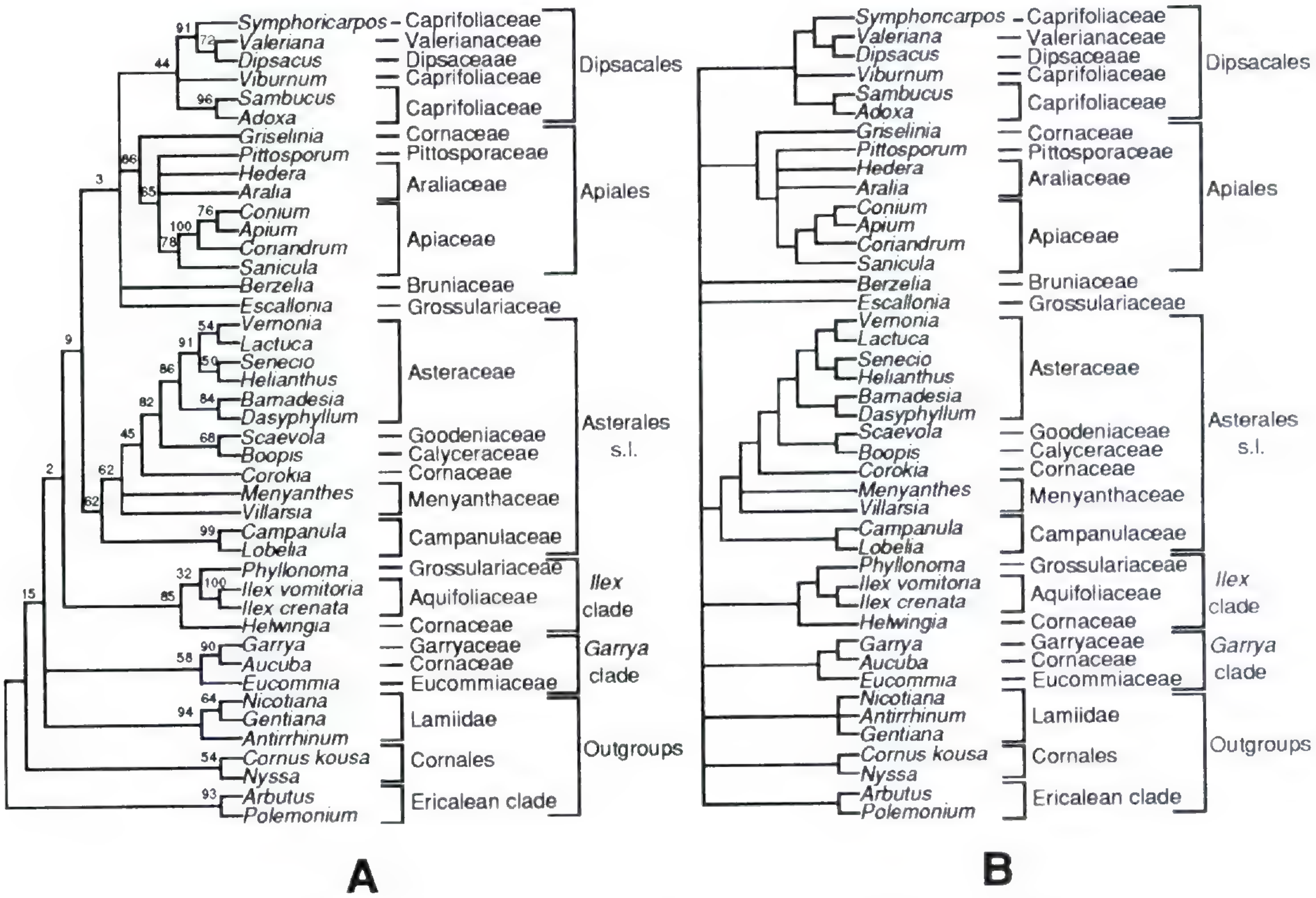


FIGURE 7.—Strict consensus trees for *rbc*L sequences representing the Asterales s.l., Apiales, and Dipsacales.—A. Island-80. Strict consensus of 80 trees (length = 1,368, C.I. = 0.39, R.I. = 0.51). Numbers above branches indicate percent occurrence of subtended clade in 100 bootstrap replicates.—B. Island-196. Strict consensus of 196 trees (length = 1,368, C.I. = 0.39, R.I. = 0.51). This consensus tree is the same as for the combined consensus of island-80 and island-196. Family designations follow Cronquist (1981) and do not imply necessarily that the entire family belongs where these representatives occur.

reliability of the results. How can one be sure that the results found represent the optimal solution for the data? How can one resolve incongruence between separate analyses conducted on similar data sets (e.g., differences between the analyses of Chase et al., 1993, this issue, and analyses presented here)? Will sampling more taxa, sampling more characters (e.g., nucleotides), or more detailed analyses of a subset of the data provide better results? It is not clear that there is a single best answer to any of these questions and when data of this nature are compiled for the first time for a group of organisms, as these are for the Asteridae (and angiosperms), there is no independent, external means for evaluating the results. Internal methods for evaluating trees (e.g., bootstrap or decay analysis) are extremely difficult to implement on a large data set. Bearing in mind that there is little in the way of rigorous, quantitative, phylogenetic hypotheses against which to evaluate these results, they should be considered preliminary, awaiting the availability of a substantially greater amount of data derived from other sources.

For the results of a cladistic analysis to provide strong support for a hypothesis, alternative hypotheses must be examined. This requires searching for multiple islands with sufficient diligence to reach other islands, if they exist. For one well-known data set of human mitochondrial DNA sequences (Vigilant et al., 1991), a reanalysis of the data yielded separate islands each having different implications with respect to the geographic origin of modern humans (Maddison et al., 1992). The initial analysis (Vigilant et al., 1991) was unable, by design, to find more than one island and, therefore, was predestined to yield one conclusion.

A total of approximately eight to ten months of computer time was spent on the several analyses reported here. Multiple islands were found whenever the appropriate search strategy was employed for each data set examined in this study. In all cases only two or three separate initial searches each of 200–2,000 random-order-entry starting points were required to find multiple islands, leaving open the possibility that additional islands, some perhaps shorter, remain to be found. Whereas it

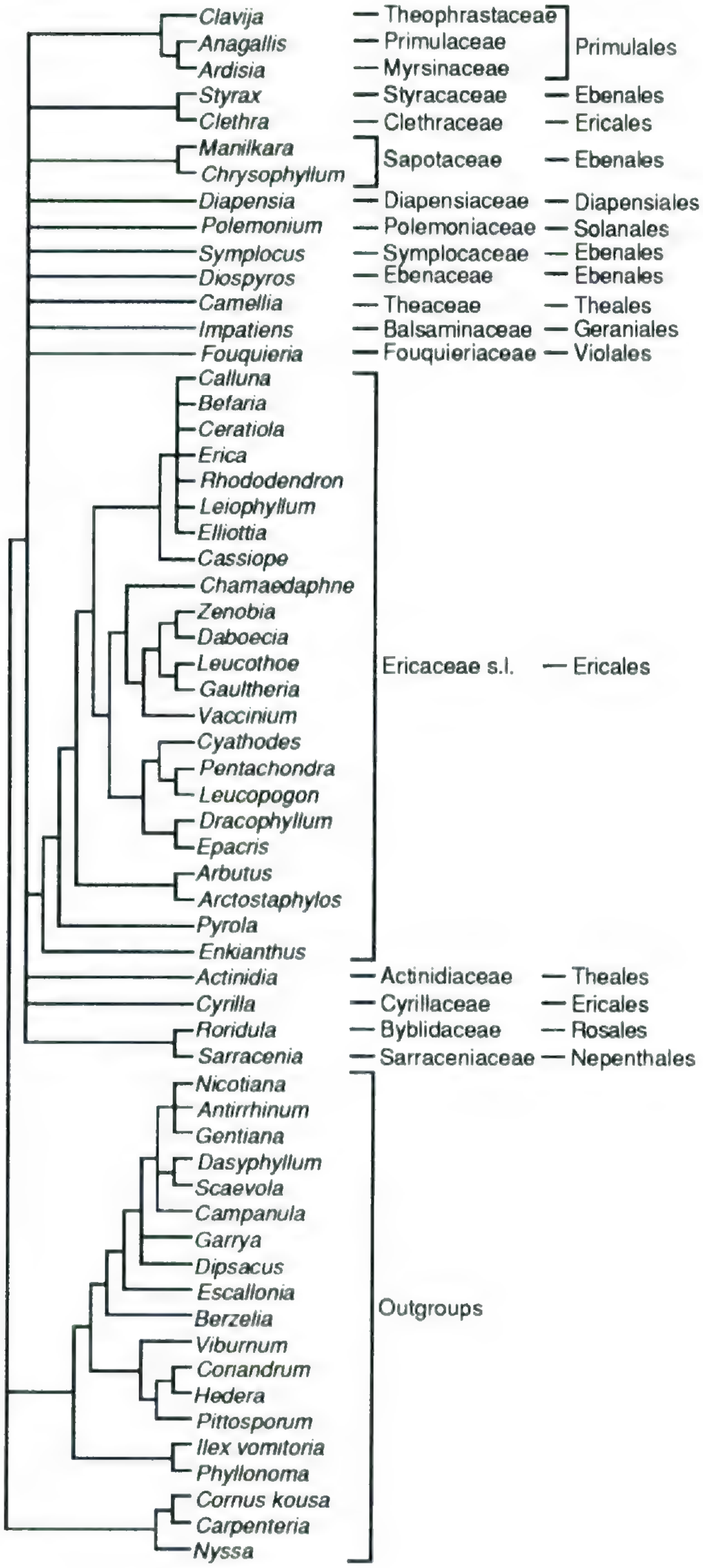


FIGURE 8. Strict consensus trees for the ericalean clade based on *rbc*L sequences.—A. Strict consensus of 969 trees combining island-612 and island-357. Resolution resides almost exclusively within the Ericaceae s.l.—B. Strict consensus of island-612 (612 trees length = 1,889, C.I. = 0.33, R.I. = 0.55).—C. Strict consensus of island-357 (357 trees length = 1,890, C.I. = 0.33, R.I. = 0.55). Relationships among outgroups and within Ericaceae s.l. are the same for both islands, thus are only indicated in A. Family designations follow Cronquist (1981) and do not imply necessarily that the entire family belongs where these representatives occur.

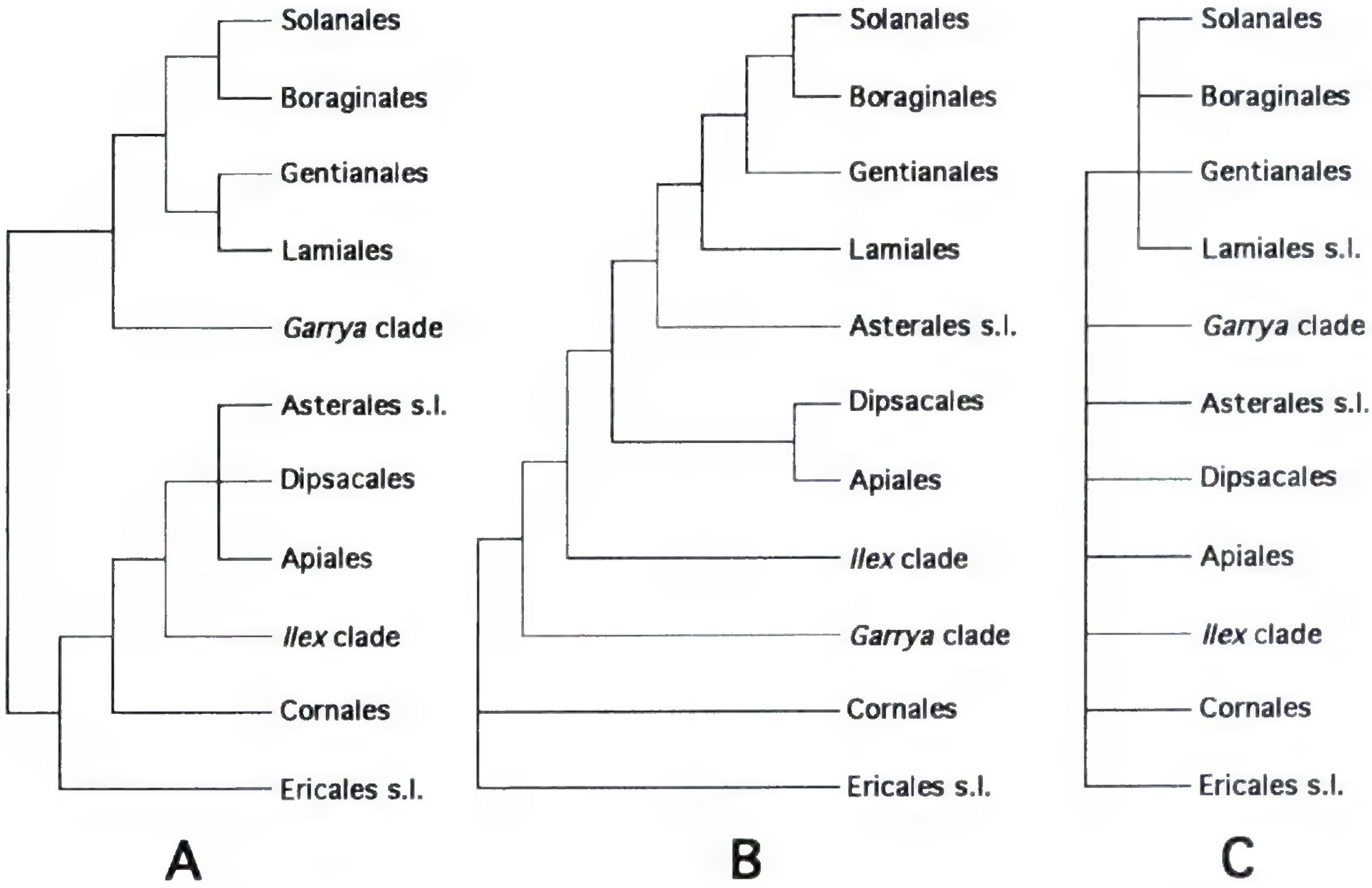


Figure 9.—Condensed cladograms representing the relationships among primary groups in the Asteridae s.l. based on *rbc*L sequences.—A. Island-102.—B. Island-2,784.—C. Combined consensus of island-102, island-2,784, and island-5,568.

is not possible to know if all islands within the Asteridae s.l. have been discovered, finding at least two islands provides a cautionary note with respect to the extent to which the findings can be used for evolutionary and systematic interpretations.

The discovery of multiple islands of trees of equal, or near-equal, length implies that there are regions of conflict in the hypotheses of relationship that derive from them. The conclusions in which we can have the most confidence are those that are shared between islands. The analysis of 105 sequences (designed to examine overall relationships within the Asteridae s.l.) and the analysis of 82 sequences (which includes numerous additional outgroup sequences, but reduced sampling within the Asteridae s.l.) both agree with the conclusions of Olmstead et al. (1992) and Chase et al. (1993) in the circumscription of a monophyletic Asteridae s.l. Within the Asteridae s.l., the three islands of trees discovered in the analysis of 105 sequences are congruent in the composition of 11 terminal groups (Fig. 9) and in the monophyly of one group comprising four of the terminal groups (Lamiidae sensu Takhtajan, 1987). Differences among islands exist both within and among these 11 groups, indicating that different cladistic patterns within monophyletic groups can influence the most parsimonious patterns among those groups. Two sequences (*Berzelia* and *Escallonia*) each fall into a specific clade in one island, but remain unresolved in the other island. Interestingly, these two sequences represent families that Hufford (1992) identified as individual branches at the base of the entire Asteridae s.l. They will be included in the discussion below with the clade to which they belong in at least one island.

The names used for groups identified here were chosen to reflect formally described taxonomic groups to which they are most closely similar. However, we consider these to be provisional names at this time, and they should not be viewed as constituting a formal classification. The 11 putatively monophyletic groups identified within the Asteridae s.l. are as follows (family, order, and subclass designations for included representatives follow Cronquist, 1981, unless otherwise noted):

(1) **Cornales.** This clade contains representatives of the Cornaceae, Hydrangeaceae, and Nyssaceae, all formerly placed in the subclass Rosidae. Several representatives placed within or near one or the other of these families in most angiosperm classification schemes are found elsewhere in the

*rbc*L tree of the Asteridae s.l. Three subgroups are identified within this clade: the Hydrangeaceae, *Cornus* (representing the Cornaceae s.s.), and the Nyssaceae. *Alangium* remains unresolved with respect to placement in either the Cornaceae s.s. or Nyssaceae (but see Xiang et al., 1993). Both Anderberg (1992) and Hufford (1992) identified this clade (including Loasaceae and Sarraceniaceae in Hufford, 1992) in their morphology-based cladistic analyses. Greater sampling and more detailed analysis of this clade shows substantial resolution based on *rbc*L sequences; see Xiang et al. (1993) and Morgan & Soltis (1993) for further discussion.

(2) **Ericalean clade.** This clade is mostly composed of former representatives of the Dilleniidae, including the orders Diapensiales, Ebenales, Ericales, Nepenthales, Primulales, Theales, and Violales (*Fouquieria*). The only non-dilleniid representatives in this clade are *Polemonium* (Polemoniaceae, Asteridae), *Roridula* (Byblidaceae, Rosidae), and *Impatiens* (Balsaminaceae, Rosidae). The clade identified here (see also Chase et al., 1993; Kron & Chase, 1993) has not been recognized in any formal classification. Within this group (Fig. 8A) representatives of the Ericaceae s.l. form a clade (Kron & Chase, 1993), as do a few pairs or triplets of sequences: *Clavija*, *Anagallis*, *Ardisia* (Primulales), *Styrax* (Styracaceae, Ebenales) with *Clethra* (Clethraceae, Ericales), *Manilkara* with *Chrysophyllum* (Sapotaceae, Ebenales), and *Sarracenia* (Sarraceniaceae, Nepenthales) with *Roridula* (Byblidaceae, Rosales). Most of the rest of the sequences in this clade are single representatives of families. This clade is noteworthy for the lack of resolution even within islands at the level of sampling represented here (Fig. 8B, C). *Actinidia* and *Roridula*–*Sarracenia* consistently occur with the Ericaceae (Fig. 8), each as sister group in one island, but do not appear as part of the clade in the consensus tree, because *Cyrilla* occurs in that clade in one island and not in the other. Considerably more work is needed before the picture of relationships within this clade can be brought into focus. See Kron & Chase (1993) for further discussion.

(3) ***Garrya* clade.** This small clade is represented by three sequences: *Garrya* (Garryaceae, Cornales), *Aucuba* (Cornaceae), and *Eucommia* (Eucommiaceae, Eucommiales, Hamamelidae). This represents a previously unrecognized group and includes species not formerly placed in the Asteridae. However, morphological and chemical features uniting these taxa and supporting their association with the Asteridae s.l. can be recognized (see below and Xiang et al., 1993).

(4) ***Ilex* clade.** This small clade is represented by four sequences: *Ilex crenata* Thunberg and *I. vomitoria* Aiton (Aquifoliaceae, Celastrales, Rosidae), *Helwingia* (Cornaceae), and *Phyllonoma* (Grossulariaceae, Rosales). This is another previously unrecognized clade, which does, nonetheless, have putative morphological synapomorphies (Morgan & Soltis, 1993) and is united with the Asteridae s.l. by the presence of unitegmic and tenuinucellate ovules. Our results, with greater sampling within the Asteridae s.l., differ from those of Morgan & Soltis (1993) in identifying *Ilex* and *Phyllonoma* as sister taxa (Fig. 7A, B). However, Morgan & Soltis (1993) emphasize that *Helwingia* and *Phyllonoma* share the unusual feature of epiphyllous inflorescences, suggesting that they may be more closely related than either is to *Ilex*.

(5) **Apiales.** This clade comprises representatives of the families Pittosporaceae, Araliaceae, Apiaceae, and *Griselinia* (Cornaceae), all formerly placed in the Rosidae. The Araliaceae and Apiaceae long have been recognized as closely related, and Dahlgren (1980) recognized the association of Pittosporaceae with the Apiales. Anderberg (1992) identified a monophyletic Apiales–Pittosporaceae in his morphology-based analysis of the Ericales and related families, whereas Hufford (1992) found no support for this union in his morphology-based analysis. The representatives of the Apiaceae included here form a monophyletic group (but see Plunkett et al., 1992), whereas *Pittosporum* and the representatives of the Araliaceae form an unresolved polychotomy with the Apiaceae. *Griselinia* is basal within this clade and represents one of several taxa formerly associated with the Cornaceae, but here found associated with various groups of Asteridae (see below and Morgan & Soltis, 1993).

(6) **Dipsacales.** This clade matches the order as circumscribed by Cronquist (1981). Within the order, *Sambucus* and *Adoxa* form a clade and *Dipsacus*, *Valeriana*, and *Symphoricarpos* form a clade. *Viburnum* forms a trichotomy with the other two clades. The Caprifoliaceae, as classically circumscribed (represented here by *Symphoricarpos*, *Viburnum*, and *Sambucus*), appear to be a paraphyletic, ancestral grade within the Dipsacales. Downie & Palmer (1992) did not identify a monophyletic Dipsacales; *Viburnum* and *Sambucus* occurred with the Asterales s.l. and the rest of the order with the Apiales (*Adoxa* was not included in their study). *Berzelia* (Bruniaceae, Rosales) occurs as the basal branch of this clade in island-2,784 (Figs. 1B, 2), but is unresolved at the base of a clade comprising the Dipsacales, Asterales s.l., and Apiales in island-102 (Fig. 1A) and in the Astera-

les–Dipsacales–Apiales analysis (Fig. 7). See Donoghue et al. (1992) for further discussion.

(7) **Asterales s.l.** This clade comprises the orders Asterales, Campanulales, and Calycerales, as well as the Menyanthaceae (Solanales), and *Corokia* (Cornaceae). In the analysis of 105 sequences of the Asteridae s.l., the Campanulaceae, Goodeniaceae, and Calyceraceae together form the sister group to the Asteraceae, whereas with greater sampling in the Asterales s.l., only the Goodeniaceae and Calyceraceae form the sister group (in agreement with "Search II" of Chase et al., 1993, and Michaels et al., 1993) with the Campanulaceae forming the basal lineage within the clade (Fig. 7). The very long terminal branch of *Campanula* (Fig. 2), when included in an analysis without the closely related sequence *Lobelia* (e.g., Fig. 1), raises the possibility of artifactual placement due to long-branch attraction (Felsenstein, 1978). When *Lobelia* also is included (Fig. 7), the long-branch problem is lessened. The Asterales s.l. have been the subject of extensive *rbc*L sequence analysis (Kim et al., 1992; Michaels et al., 1993). Michaels et al. (1993) report a detailed analysis of this group in which the Campanulaceae are excluded from both the sister clade of the Asteraceae (bootstrap value—86% and decay index—four steps) and from the clade comprising the Asteraceae and its sister group (84%, four steps). A bootstrap analysis was performed on the 43-sequence data set used in this study with similar results (Fig. 7A). The fact that "Search I" of Chase et al. (1993) included both *Campanula* and *Lobelia* in the sister group to the Asteraceae indicates that "Search I" probably did not reach maximum parsimony for this clade. Anderberg's (1992) morphological analysis identified the Campanulaceae as sister group to the Asteraceae, with the Goodeniaceae–Calyceraceae as the next branch. The association of the Menyanthaceae with the Asterales was not predicted by conventional classifications, but was identified by Olmstead et al. (1992) based on *rbc*L sequences and by Downie & Palmer (1992) based on analysis of cpDNA inverted repeat restriction sites, and has now been accepted by Thorne (1992). See Michaels et al. (1993) for further discussion. *Escallonia* (Grossulariaceae, Rosales) occurs as the basal branch of this clade in island-102 (Fig. 1A), but is unresolved at the base of a large clade comprising the Asterales s.l., Apiales, Dipsacales, and Lamiidae (sensu Takhtajan, 1987) in island-2,784 (Figs. 1B, 2) and island-5,568 (not shown).

(8) **Gentianales.** This clade comprises the Apocynaceae, Asclepiadaceae, Gentianaceae, Loganiaceae, and Rubiaceae. Of recent classifications, Thorne's (1992) is the only one fully in accord with this circumscription. Others have included Oleaceae and Menyanthaceae (in superorder Gentiananae; Dahlgren, 1980; Takhtajan, 1987), or excluded Rubiaceae (Cronquist, 1981). The monophyly of this group is supported by the analysis of restriction site variation in the cpDNA inverted repeat (Downie & Palmer, 1992). Within the clade, the representatives of the Rubiaceae and Apocynaceae s.l. (including the Asclepiadaceae) each form monophyletic groups, as does a group containing representatives of the Gentianaceae and two members of the Loganiaceae (*Anthocleista* and *Fagraea*). The Loganiaceae represent a heterogeneous assemblage, with members in several lineages of the Gentianales (Bremer & Struwe, 1992).

A comparison of the results of the analysis of the Asteridae s.l. data set with those of the Lamiidae data set reveals an interesting and possibly common artifact of analysis when a sequence generating a long terminal branch is included (as with *Campanula* above). In the analysis with fewer Gentianales (Figs. 1, 2), *Gentiana* is basal, with *Gelsemium* next, then *Apocynum*, and *Pentas* and *Spigelia* are terminal. *Pentas* (Rubiaceae) has a very long terminal branch (Figs. 2, 10). In the analysis with 13 Gentianales included (Figs. 5, 6), almost the exact reverse order is obtained with Rubiaceae basal (Rubiaceae is also basal in Downie & Palmer, 1992). A possible explanation for this difference is that in the analysis with fewer sequences, spurious similarity between one of the terminal taxa (*Gentiana*) and the sister group "pulled" that sequence to the base of the clade. Homologous similarity within the clade then resulted in a reverse branching order. In other words, the branching topology within the clade remains essentially the same, but the clade attaches to the rest of the tree at a different point. Adding more sequences along each lineage in the clade (e.g., including *Chiococca* in the Rubiaceae) increases the probability that parsimony analysis will correctly interpret homology, resulting in the correct attachment of the clade to the tree. A local analysis of the Gentianales was conducted to examine internal support within the clade. The 13 representatives of the Gentianales were included with seven outgroups (*Garrya*, *Eucommia*, *Nicotiana*, *Heliotropium*, *Antirrhinum*, *Catalpa*, and *Ligustrum*) and bootstrap and decay analyses were conducted. Seven equally parsimonious trees were found (Fig. 10), with the majority rule consensus tree and bootstrap majority rule consensus trees having the same topology as in Figures 5 and 6. The results support groups representing the Gentianaceae,

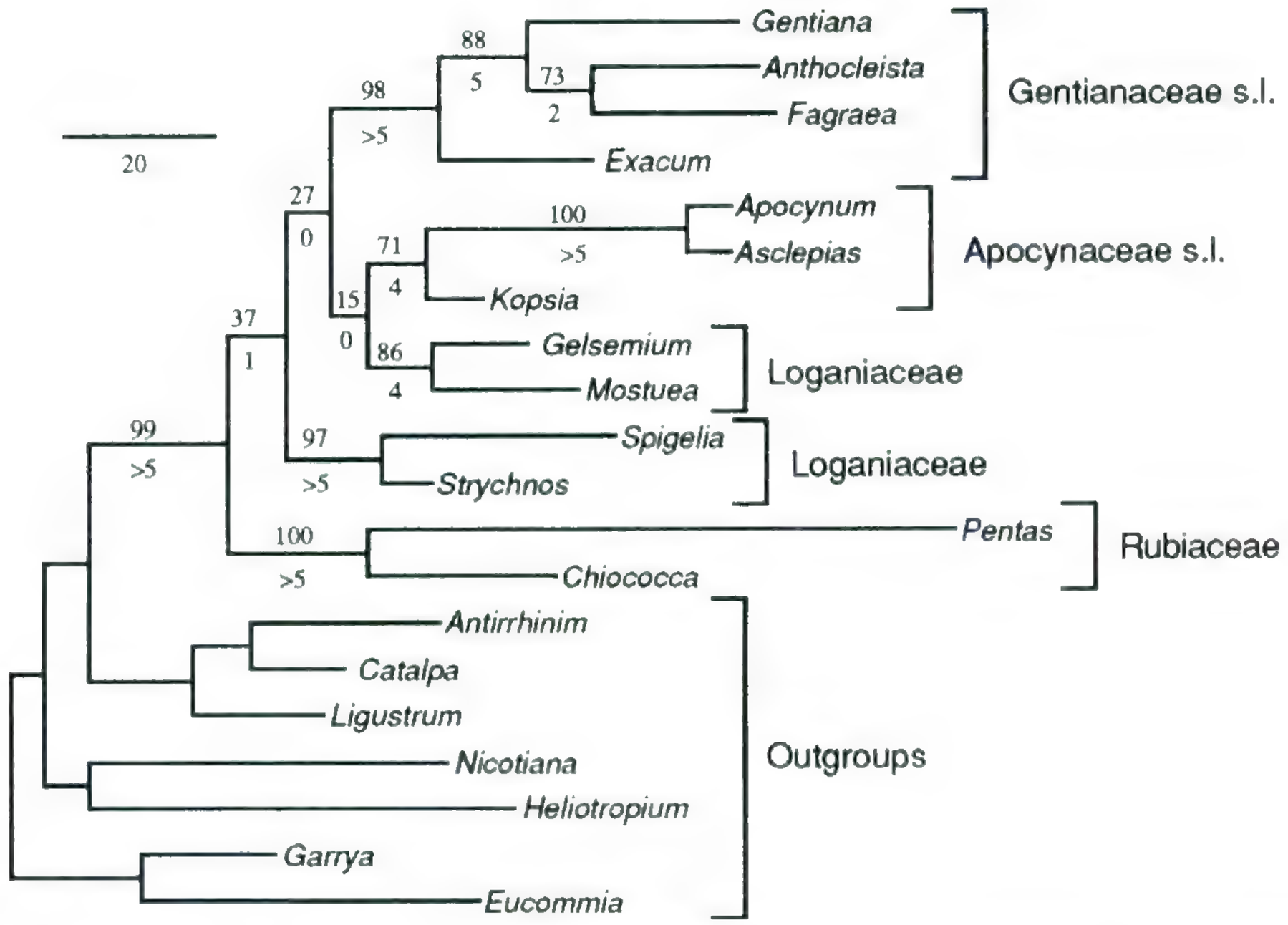


FIGURE 10. Majority-rule consensus of seven equal-length trees of the Gentianales based on *rbc*L sequences and rooted using seven outgroups from the Solanales, Boraginales, Lamiales s.l., and the *Garrya* clade. This tree is equivalent to the topology found in the analysis of the entire Lamiidae data set (Fig. 5) and represents the bootstrap majority-rule consensus. Internal support for groups within the Gentianales is indicated by branch lengths proportional to the scale bar in the upper left and by bootstrap values above and decay indices below internodes subtending clades. A decay index of zero indicates the node collapses in the strict consensus of the seven trees.

Apocynaceae s.l., Rubiaceae, and two separate groups of Loganiaceae (*Gelsemium–Mostuea* and *Spigelia–Strychnos*), but provide little support for any internal groupings.

(9) **Solanales.** This clade is comprised of the Convolvulaceae, Solanaceae, and *Montinia* (Grossulariaceae). Comparable groups exist in the classifications of Dahlgren (1980) and Thorne (1992), except for the inclusion of the Polemoniaceae by Dahlgren (1980). Both Takhtajan (1987) and Thorne (1992) included the Polemoniaceae in a more inclusive group with the Solanales and Boraginales. *Montinia*, not previously suggested to belong to this group on the basis of conventional characters, is basal to the Solanaceae and Convolvulaceae (see below and Morgan & Soltis, 1993). The Solanales and Boraginales form a clade in most analyses, but in island-5,568 (not shown) the Solanales are sister to a clade comprising the Boraginales and Gentianales.

(10) **Boraginales.** This clade comprises the Hydrophyllaceae and Boraginaceae. Groups comparable to this exist in most recent angiosperm treatments (Dahlgren, 1980; Takhtajan, 1987; Thorne, 1992; but not Cronquist, 1981). With the limited sampling currently available, the Boraginaceae appear paraphyletic and the Hydrophyllaceae a monophyletic derivative from them. However, the putatively primitive borages in the woody subfamilies Ehretioideae and Cordioideae have not been sampled for *rbc*L sequences. The Boraginales are sister group to the Solanales in most analyses reported here and in the analyses of Olmstead et al. (1992) and Chase et al. (1993), but are sister group to the Gentianales in island-5,568 (not shown).

(11) **Lamiales s.l.** This clade is comprised of the orders Scrophulariales, Lamiales, and Callitrichales, as well as *Byblis* (Byblidaceae, Rosales) and was recognized by Olmstead et al. (1992) and Downie & Palmer (1992) as monophyletic. This group is recognized by Dahlgren (1980), Takhtajan (1987), and Thorne (1992), but all three treatments maintain a distinction between the Lamiales s.s. and the Scrophulariales. As was pointed out previously (Olmstead et al., 1992), the Scrophulariales are not a monophyletic group. In addition, results presented here (Fig. 5) and results of current work (Wagstaff & Olmstead, unpublished data) suggest that the Lamiales s.s. also may not be monophyletic. Therefore, it seems appropriate not to subdivide this group at present. *Buddleja* and *Nicodemia* have been considered congeneric and placed either in the Buddlejaceae (e.g., Cronquist, 1981) or Loganiaceae (e.g., Mabberley, 1987). In

this analysis, they both clearly belong in the Lamiales s.l. rather than the Gentianales, but the two sequences do not appear to be closely related. Likewise, the Oleaceae have been placed either in the Scrophulariales (e.g., Cronquist, 1981), Gentianales (e.g., Stebbins, 1974), or in their own order, Oleales, allied with the Gentianales (Dahlgren, 1980; Takhtajan, 1987). Based on this *rbc*L analysis the Oleaceae appear to be the basal branch of the Lamiales s.l.

As with the ericalean clade, the strict consensus of the two islands discovered in the analysis of the Lamiidae reveals little resolution within the Lamiales s.l. However, unlike the ericalean clade, where there is little resolution within either island, in this group each island exhibits substantial resolution with particular sequences or small groups occurring in very different places in the two islands. This clade is more densely sampled than most other clades in the Asteridae s.l. Most of the groups that are congruent between islands consist of multiple representatives of large families, including the Acanthaceae, Scrophulariaceae, and Labiatae s.l. The Lamiales s.s. (Labiatae and Verbenaceae) may not be a monophyletic group, as was suggested previously based on a more limited sampling of *rbc*L sequences (Olmstead et al., 1992). Most of the representatives of the Lamiales s.s. form a monophyletic group with no clear distinction between the traditional Labiatae and Verbenaceae. In this respect the clade closely fits the circumscription of the family first suggested by Junell (1934) and recently revived by Cantino et al. (1992). However, *Verbena*, the sole representative of subfamily Verbenoideae in this analysis, is placed closest to *Nicodemia* in a position removed from the rest of the Lamiales in island-135 (Fig. 5) and basal to them in island-1,350 (Fig. 6A). The Lamiales s.l. are the subject of continuing research (Hedrén et al., in prep.; Scotland & Olmstead, in prep.; Wagstaff & Olmstead, unpublished).

These results are fully congruent with those of Olmstead et al. (1992) for relationships among clades within the Asteridae s.l. However, in that study the Dipsacales and Apiales form a clade and together with the Asterales s.l. form another, more inclusive, clade, whereas in this study relationships among the three groups remain unresolved. A bootstrap analysis (Olmstead et al., 1992) suggested moderately strong support (79%) for the Dipsacales–Apiales clade and weaker support for the Asterales–Dipsacales–Apiales (61%). The results of a bootstrap analysis conducted here (Fig. 7) indicate 11% (not indicated on Fig. 7) and 9% values, respectively, for the same two groups. These much lower values reflect the much greater taxon sampling density of this study (see Olmstead et al., 1992, for discussion of this effect). The Asterales–Dipsacales–Apiales clade also is found in both analyses of Chase et al. (1993). Differences in sampling and search strategies may account for the different results obtained in the three studies. A clade comprising the Dipsacales and Apiales minus *Viburnum* and *Sambucus* was found by Downie & Palmer (1992), but their study did not support a united Asterales–Dipsacales–Apiales. No clade comprising any combination of these groups was found by Hufford (1992).

The last four clades, Gentianales, Solanales, Boraginales, and Lamiales s.l., together form the only higher-order clade that is congruent between all three islands. These orders form Takhtajan's (1987) subclass Lamiidae. This group is one of the most strongly supported clades in bootstrap analyses of *rbc*L data (94%—Olmstead et al., 1992; 94%—Morgan & Soltis, 1993) and also was identified in the cpDNA inverted repeat restriction site analysis of Downie & Palmer (1992). Relationships among the four primary clades within the Lamiidae remain unresolved in Olmstead et al. (1992), Downie & Palmer (1992), and in the strict consensus of the 3,900 trees found in "Search II" of Chase et al. (1993). In the analysis of the Asteridae s.l., the Lamiales s.l. are basal in island-2,784 (Figs. 1B, 2) and island-5,568 (not shown), whereas a clade comprising the Solanales and Boraginales is basal in island-102 (Fig. 1A). In the Lamiidae analysis, with greater sampling within the group, the Solanales–Boraginales appear basal in both islands found. However, the strength of the latter conclusion is weakened by the reduced outgroup sampling in that analysis. Morgan & Soltis (1993), including a sequence for the saxifragaceous genus *Vahlia* at the base of the Lamiales s.l., identify the Gentianales as the basal branch within the Lamiidae.

The analyses of Chase et al. (1993) and the inverted repeat restriction site analysis of Downie & Palmer (1992) identify the *Garrya* clade as the sister group to the Lamiidae. That result also was obtained in island-102 and both of the shortest islands resulting from the analysis of the Lamiidae data set. However, island-2,784, island-5,568, and both of the islands one step longer than the shortest in the Lamiidae analysis do not support the sister group relationship between the Lamiidae and the *Garrya* clade.

"Search II" of Chase et al. (1993) identified the small clade of *Dillenia* and *Vitis* as sister group to the Asteridae s.l., but our results suggest that the sister group is a large clade comprising most

of the Rosidae and Dilleniidae (including *Dillenia* and *Vitis*). That this relationship remains uncertain is indicated by the short internode length between the divergence of this small branch from the main lineage of the Rosidae and in adjacent internodes (Fig. 4). Thus, the question of the sister group to the Asteridae s.l. remains unresolved, but the conclusion that this clade originated relatively early in the diversification of the higher dicots (Olmstead et al., 1992) is supported here and in the analyses of Chase et al. (1993).

These results and those of Olmstead et al. (1992) both leave the base of the Asteridae s.l. unresolved. Island-102 in this study identified the Lamiidae and *Garrya* clades as the basal branch, whereas island-2,784 and island-5,568 were unresolved at the base, with either the Cornales or the Cornales–ericalean groups as possible basal branches. The analyses of Chase et al. (1993) identify the Cornales as basal within the Asteridae s.l. and the ericalean clade the next branch. The cpDNA inverted repeat restriction site study of Downie & Palmer (1992) identified the ericalean group as basal, then the Dipsacales–Apiales, Asterales s.l., Cornales, and Lamiidae, but their study had few representatives of the ericalean group (Polemoniaceae and Fouquieriaceae) and fewer outgroups. Hufford (1992) identified three solitary families as individual basal branches (Bruniaceae, Alseuosmiaceae—not included in *rbc*L analyses, and Escalloniaceae), then the Cornales, ericalean group, and the traditional Asteridae. Anderberg (1992) identified the ericalean group as basal, with no resolution among the remaining groups, but his study also suffered from extremely limited outgroup sampling, which compromises any conclusions at this level.

These results represent a detailed, but by no means exhaustive, search for optimal solutions to the *rbc*L phylogeny of the Asteridae s.l. Our two-tiered approach of broadly sampling the entire Asteridae s.l. and sampling more densely within recognized clades offers opportunities to explore patterns of relationship in greater detail at various levels. The discovery of multiple islands in each of the subsets of the data in which a search for islands was conducted indicates that analysis of *rbc*L data (and probably most large complex DNA sequence data sets) must include an appropriate search strategy for finding multiple islands. The presence of multiple islands, which, by their nature, imply different patterns of relationship, indicates that the *rbc*L data by themselves cannot resolve relationships at all levels within the Asteridae s.l. Congruence between analyses at different hierarchical levels is encouraging, although it does not in any sense constitute a test of the results found in one analysis, because the same data form the basis for all analyses. In contrast, incongruence between analyses at different levels (e.g., the inverted topology of the Gentianales in one analysis relative to another) demands an explanation.

In addition to the two-tiered hierarchical analyses reported here for the Asteridae s.l., the analyses of Chase et al. (1993) present a third tier available for comparison (i.e., angiosperms and seed plants). The same 11 primary clades identified here in the Asteridae s.l. are identified in that analysis. However, the pattern of relationships among primary lineages within the Asteridae s.l. implied by the analyses of Chase et al. (1993) is incongruent with each island found in the analysis of the Asteridae s.l. data set. Two important differences exist between these analyses: (1) the analyses of Chase et al. (1993) have greater sampling of ingroup and outgroup sequences in a single analysis, and (2) the smaller data sets used in this study were analyzed more fully for shortest trees and multiple islands. During the search for multiple islands in the Asteridae s.l., each search became "stuck" for a long time on a plateau of trees longer than was ultimately found by that search. In one search, a plateau three steps longer was searched with over 4,600 trees found at that length; the consensus tree was congruent with the results reported by Chase et al. (1993) for the Asteridae s.l. The seed plant analysis was conducted with NNI swapping and a ceiling of 3,900 trees, of which only three were examined with TBR swapping and with MULPARS off. This search strategy is unlikely to enable one to get off a plateau such as those encountered in our searches. This suggests that, as was explicitly admitted in Chase et al. (1993) for their broad analyses in general, their results may represent a suboptimal plateau with respect to the Asteridae s.l.

## CONGRUENCE WITH CONVENTIONAL CHARACTERS

The identification of biological traits, other than nucleic acid bases at particular positions in a DNA sequence, which are congruent with the results of a DNA sequencing study, provides potential synapomorphies and important validation for groupings suggested by the molecular analysis. The *rbc*L analysis of the Asteridae offers the opportunity to examine some of the critical characters that have been used in traditional classifications.

The most visible feature commonly associated with the Asteridae is the sympetalous corolla. It

formed the basis for a major group of dicots, the Gamopetalae (de Candolle, 1813), in early classifications. Many families characterized by sympetaly, which have been segregated into different subclasses in many recent classifications (e.g., Cronquist, 1981), are reunited in the *rbc*L tree in the clade designated Asteridae s.l. The *rbc*L tree, however, includes several polypetalous groups, including the Cornales (as broadly defined by Cronquist, with representatives found in several clades), Apiales, Grossulariaceae (*Escallonia* and *Phyllonoma*), Hydrangeaceae, and Pittosporaceae (*Pittosporum*). The distribution of these polypetalous taxa on the *rbc*L tree makes problematic the interpretation of the origin of sympetaly. The Cornales and the *Garrya* clade are the only groups of the 11 discussed above that are consistently polypetalous. Polypetalous groups are basal to otherwise predominantly sympetalous groups in many important clades. For examples of this pattern note *Corokia* with the Asterales s.l., *Vahlia* with the Lamiales s.l. (see Morgan & Soltis, 1993), and *Berzelia* with the Dipsacales. A few sequences represent families in which both sympetaly and polypetaly occur (e.g., *Camellia*—Theaceae, *Berzelia*—Bruniaceae). Some polypetalous taxa (e.g., *Sarracenia* and *Montinia*) are embedded within sympetalous clades (e.g., Ericales and Solanales, respectively). Hufford (1992) considered sympetaly to be a synapomorphy for his Cornifloraeasterid group (comparable to our Asteridae s.l.) exclusive of Bruniaceae (*Berzelia* in our study).

One possible explanation for the observed pattern of corolla fusion is that the Asteridae s.l. originally diversified as a polypetalous clade with subsequent evolution of sympetaly in several lineages. In this scenario, the polypetalous taxa near the base of many clades represent plesiomorphic relicts. However, an alternative hypothesis may be that sympetaly evolved early in the Asteridae s.l. and, during the early diversification of the clade, corolla fusion remained a developmentally labile trait before becoming rigidly canalized (Donoghue, 1989; Olmstead et al., 1992). In this scenario, polypetalous taxa represent the occasional reversion to polypetaly and would be expected to be found primarily near the base of clades. The pattern of corolla development in some groups (e.g., Apiales, Erbar, 1991) suggests that reversal from sympetaly to polypetaly has occurred (Olmstead et al., 1992). This is an example of an area in which morphology deserves renewed investigation as a result of hypotheses derived from a molecular cladogram. The distribution of corolla fusion among the groups and the existence of tree islands make difficult any assessment of corolla evolution. It appears that multiple origins are likely, but that some reversals may have occurred as well.

The presence of tenuinucellate ovules with a single integument has been associated with the Asteridae s.s. (e.g., Cronquist, 1981), but has many exceptions outside the narrow circumscription of the Asteridae. However, the broadly circumscribed Asteridae s.l. encompass the large majority of those exceptions. A single integument (the result of fusion or loss of one integument) characterizes nearly all groups in the Asteridae s.l., except some members of the ericalean clade (e.g., Primulales and some Ebenales). The tenuinucellate condition generally is considered to be derived from the crassinucellate condition in angiosperms and also characterizes most members of the Asteridae s.l.; exceptions include the *Garrya* clade and the Cornaceae and relatives (but not the Hydrangeaceae). The trait "crassinucellate ovule" encompasses a wide range of expression (Davis, 1966; Young & Watson, 1970) and is apparently derived from tenuinucellate ancestors where it occurs in the Asteridae s.l. Hufford (1992) identified single integument as a synapomorphy for his Cornifloraeasterid group and tenuinucellate ovules as a synapomorphy to the same group exclusive of the Bruniaceae.

The distribution of iridoid compounds has influenced heavily the classification of Dahlgren (1980), and the presence/absence of iridoids led Jensen et al. (1975) to reject the traditional Asteridae "as a natural group." Most discussions of the systematic significance of iridoids rely on their evolutionarily derived condition and the implication that the iridoids identify a monophyletic group (e.g., Jensen, 1992). This leads to conflicts with groupings based on other characters. The distribution of iridoids in the Asteridae s.l. suggests that iridoids form a synapomorphy for the entire clade comprising the Asteridae s.l. The distribution of iridoids in the ericalean clade combined with the lack of resolution in that clade makes it difficult to assess the basal state for the clade with respect to iridoids. The pattern of relationships depicted in island-2,784 (Figs. 1B, 2) includes the possibility that the ericalean clade is basal within the Asteridae, thereby leaving open the possibility that if that clade is non-iridoid-containing at its base then iridoids may have evolved twice in the Asteridae s.l. However, it seems that the presence of iridoids is the basal condition in the Asteridae s.l. and the absence of iridoids is best interpreted as losses in several lineages, including the Primulales, Ebenales and relatives (within the ericalean clade), the Apiales, the Campanulaceae (Asterales s.l.), the Asteraceae, and

the Solanales. Additional losses within the Asteridae s.l. are known (e.g., within the Gesneriaceae and Labiatae subfam. Nepetoideae). The presence of simple iridoids in some members of the Hamamelidae (e.g., *Liquidambar*, *Daphniphyllum*), which exhibit morphological, embryological, and *rbc*L evidence incongruent with a placement in the Asteridae s.l., suggests that iridoids have evolved more than once.

The distribution of iridoids in plants has proven to be problematic for systematics, but as phylogenetic hypotheses become more refined, the distribution of iridoids and other secondary compounds may make more sense. For example, Jensen (1992) presented an apparent contradiction in the Oleaceae, which contain both seco-iridoids (grouping them with the Gentianales) and verbascosides (grouping them with the Lamiales s.l.). The *rbc*L tree places the Oleaceae at the base of the Lamiales s.l. clade, suggesting that the seco-iridoids are a plesiomorphic trait shared with the Gentianales, whereas the verbascosides are a synapomorphy uniting them with the Scrophulariales and Lamiales.

### PROBLEMS MERITING FURTHER INVESTIGATION

The *rbc*L tree of the Asteridae s.l. suggests several unexpected groups that merit further investigation. For example, *Polemonium* (Polemoniaceae, Asteridae) is grouped (e.g., Fig. 1A) with *Diapensia* (Diapensiaceae, Dilleniidae). These two taxa share many characters, including fused, pentamerous perianths, three fused carpels with numerous ovules, axile placentation, ovules that are unitegmic and tenuicellate, an annular disk at the base of the ovary, and tetrasporangiate anthers opening by longitudinal slits. There are some differences in the secondary compounds reported for the two families, but both are congruent in the absence of iridoids and the presence of calcium oxylate crystals. *Diapensia* differs from *Polemonium* in having a second staminal whorl, a character shared with many members of the Dilleniidae, but in *Diapensia* the whorl opposite the petals is reduced to staminodia. The loss of staminodia in the Diapensiaceae would result in flowers indistinguishable from Polemoniaceae and, based on traditional criteria, assignable to the Asteridae rather than the Dilleniidae (e.g., in the system of Cronquist, 1981). The distribution of the Diapensiaceae is circumboreal at high latitudes, extending into temperate Asia. This suggests that the Polemoniaceae may represent the temperate North American derivatives of the Diapensiaceae.

The clade composed of *Garrya*, *Aucuba*, and *Eucommia* is an unanticipated grouping. However, all three taxa are dioecious and produce the iridoid aucubin. *Garrya* and *Aucuba* have similar pollen and are alike in producing petroselinic acid and in having a single whorl of stamens alternate with the petals (a character shared with the Asteridae s.s. and relatives (e.g., Apiales)). *Eucommia* lacks a corolla, but contains iridoids, has a single integument, and has a gynoecial structure that is virtually identical to that of *Garrya*, a unilocular ovary with two pendulous ovules and two style branches (*Aucuba* also has a unilocular ovule).

In several clades, a single taxon stands apart from the others, with respect to many conventional characters. Two examples are illustrative. *Griselinia* (Cornaceae) is united with the Apiales, but differs in having crassinucellate ovules, iridoids, and a single ovule. *Montinia* is perhaps the most unusual anomaly in this respect. It falls out in the Solanales, from which it differs in many respects (see Morgan & Soltis, 1993). *Griselinia* is basal within its clade, suggesting that its distinctive characters may be either plesiomorphic or autapomorphies not shared with the rest of the clade. *Montinia* appears basal within the Solanales, but embedded well within the Lamiidae, thereby making the case for plesiomorphy more difficult. Cases of anomalous results such as these demand further study, both molecular and morphological, to confirm or reject the placements suggested by these results.

## CONCLUSIONS

The results presented here and elsewhere in this issue (e.g., Xiang et al., 1993) represent another step toward a molecular-based phylogeny for the Asteridae s.l. It is clear from the existence of multiple equally parsimonious solutions, some different enough to belong to different islands using a TBR-swapping, heuristic search strategy, that we still have a long way to go to resolve many important questions. Conclusions that appear to be strong, based on the common occurrence of groups in different islands and in results of analyses at different hierarchical levels or of different data sets (Downie & Palmer, 1992; Hufford, 1992; Anderberg, 1992), include the following. (1) There exists a monophyletic Asteridae s.l. containing some elements not formerly assigned to the Asteridae. (2) The Lamiidae (sensu Takhtajan, 1987) are a monophyletic group comprising four separate clades, the Gentianales, Solanales, Boraginales, and Lamiales s.l. (including the Scrophulariales). (3) Eleven ter-

minal clades are congruent among all trees and all islands, including the four comprising the Lamiidae, the Asterales s.l., Dipsacales, Apiales, Cornales, an ericalean clade (including representatives of the Ebenales, Primulales, etc.), and two small clades herein referred to as the *Garrya* clade and *Ilex* clade. (4) With the exception of the Lamiidae, relationships among these primary lineages remain unresolved. (5) There is substantial resolution within many of these 10 clades (e.g., Apiales, Asterales s.l., Cornales, Dipsacales, Solanales), but not for others (e.g., ericalean clade, Gentianales, Lamiales s.l.). (6) Unitegmic and tenuinucellate ovules appear to be synapomorphies for the Asteridae s.l. (7) Sympetaly and the presence of iridoids also may be basal traits for the Asteridae s.l., but additional resolution is needed to distinguish multiple origins from a single origin with subsequent reversals.

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# PHYLOGENETIC RELATIONSHIPS OF *CORNUS* L. SENSU LATO AND PUTATIVE RELATIVES INFERRED FROM *rbc*L SEQUENCE DATA[1]

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## ABSTRACT

A parsimony analysis of 46 *rbc*L sequences was performed to evaluate relationships among *Cornus* and putative relatives, as well as among subgroups within *Cornus*. Our results indicate that *Alangium*, nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*), mastixioids (*Diplopanax* and *Mastixia*), *Curtisia*, and genera of Hydrangeaceae are the closest relatives of *Cornus*. These taxa, plus *Cornus*, constitute a "cornaceous clade," which differs from all previously proposed *Cornus* alliances. Within this cornaceous clade, four major lineages were identified; (i) *Cornus Alangium*, (ii) nyssoids–mastixioids, (iii) *Curtisia*, and (iv) hydrangeoids. The relationships among the four major lineages within the cornaceous clade remain unresolved. Sequence data from *rbc*L also reveal that *Corokia*, *Helwingia*, *Aucuba*, *Garrya*, and *Griselinia*, previously placed in Cornaceae by some authors, are only distantly related to *Cornus* and other members of the cornaceous clade. Four major lineages were identified within *Cornus* by *rbc*L sequence data, but relationships among these groups are incompletely resolved.

Relationships among members of the dogwood family (Cornaceae) have long been problematic due to the morphological diversity of the family. There is, for example, no consensus regarding the circumscription of the family; from 1 to 15 genera have been ascribed to Cornaceae by various authors. The troubled taxonomic history of Cornaceae is briefly reviewed below and summarized in Table 1.

Harms (1898) included 15 genera divided among seven subfamilies in his Cornaceae (Table 1), a treatment that largely followed Hooker (1867). Of these 15 genera, by far the largest and most widespread is *Cornus*, which comprises approximately 45–60 species. Many of the remaining 14 genera are small and/or localized in geographic distribution (Table 2). The considerable debate concerning the composition of Cornaceae is illustrated by the fact that 11 of the 15 genera included in Harms's (1898) Cornaceae have been treated as monotypic families by at least one author based on one or several distinctive morphological features (all original references cited in Takhtajan, 1987, except Chen, 1988): *Davidia* (Li, 1955), *Camptotheca* (Chen, 1988), *Mastixia* (Calestani, 1905), *Aucuba* (Agardh, 1858), *Curtisia* (Takhtajan, 1987), *Garrya* (Lindley, 1834), *Alangium* (de Candolle, 1828), *Melanophylla* (Takhtajan ex Airy Shaw, 1972), *Griselinia* (Takhtajan, 1987), *Helwingia* (Decaisne, 1836), and *Toricellia* (Hu, 1934).

For brevity, we will review only the treatments of Takhtajan (1980, 1987), Cronquist (1981, 1988), and Eyde (1988), because they illustrate well the magnitude of the differences among proposed taxonomic schemes regarding the treatment of Cornaceae and putative relatives. Takhtajan (1980) retained only *Cornus*, *Curtisia*, and *Mastixia* in Cornaceae, placing them in three separate subfamilies (Table 1). Many of the genera originally placed in Cornaceae by Harms (1898) were treated as distinct families and considered to be only distantly related to *Cornus* (e.g., *Corokia*, *Griselinia*, *Helwingia*, *Melanophylla*, *Kaliphora*, and *Toricellia*) by Takhtajan (1980) (Table 1). More re-

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TABLE 1. Comparison of taxonomic treatments of *Cornus* and putative relatives. Genera are not listed under monotypic families and subfamilies. An asterisk (*) indicates a family or an order that contains several genera or families, but only the genus or family listed has been considered a *Cornus* relative by some taxonomists. Hutchinson (1967) and Takhtajan (1987) divided *Cornus* into six segregate genera; for simplicity, only *Cornus* is listed below in their treatments.

| Harms (1898) | Wangerin (1910) | Hutchinson (1967) | Takhtajan (1980) | Cronquist (1981) | Takhtajan (1987) | Eyde (1988) |
|---|---|---|---|---|---|---|
| Cornaceae | Garryaceae | Araliales | Saxifragales* | Cornales | Hydrangeales* | Cornaceae |
| Garryoideae | Nyssaceae | Cornaceae | Escalloniaceae* | Alangiaceae | Argophyllaceae* | Nyssoideae |
| Nyssoideae | *Nyssa* | *Aucuba* | *Corokia* | Nyssaceae | *Corokia* | *Nyssa* |
| *Nyssa* | *Camptotheca* | *Cornus* | | *Nyssa* | Griseliniaceae | *Camptotheca* |
| *Camptotheca* | *Davidia* | *Corokia* | Cornales | *Camptotheca* | Melanophyllaceae | *Davidia* |
| Davidioideae | Alangiaceae | *Curtisia* | Davidiaceae | *Davidia* | *Melanophylla* | Mastixioideae |
| Alangioideae | Cornaceae | *Griselinia* | Nyssaceae | Cornaceae | *Kaliphora* | Cornoideae |
| Mastixioideae | Mastixioideae | *Kaliphora* | *Nyssa* | *Aralidium* | | |
| Curtisioideae | Curtisioideae | *Melanophylla* | *Camptotheca* | *Aucuba* | Cornales | |
| Cornoideae | Cornoideae | *Toricellia* | Alangiaceae | *Cornus* | Davidiaceae | |
| *Aucuba* | *Aucuba* | Alangiaceae | Cornaceae | *Corokia* | Nyssaceae | |
| *Cornus* | *Cornus* | Garryaceae | Cornoideae | *Curtisia* | *Nyssa* | |
| *Corokia* | *Corokia* | Nyssaceae | Curtisioideae | *Griselinia* | *Camptotheca* | |
| *Griselinia* | *Griselinia* | *Nyssa* | Mastixioideae | *Helwingia* | Cornaceae | |
| *Helwingia* | *Helwingia* | *Camptotheca* | Aucubaceae | *Kaliphora* | Curtisiaceae | |
| *Kaliphora* | *Kaliphora* | *Davidia* | Garryaceae | *Mastixia* | Mastixiaceae | |
| *Melanophylla* | *Melanophylla* | Araliaceae* | Melanophyllaceae | *Melanophylla* | Aucubaceae | |
| *Toricellia* | *Toricellia* | *Helwingia* | *Melanophylla* | *Toricellia* | Garryaceae | |
| | | Caprifoliaceae | *Kaliphora*? | Garryaceae | Alangiaceae | |
| | | | Griseliniaceae | | Aralidiales | |
| | | | Toricelliaceae | | Toricelliales | |
| | | | Helwingiaceae | | Apiales* | |
| | | | | | Helwingiaceae | |

cently, Takhtajan (1987) removed *Curtisia* and *Mastixia* from Cornaceae and recognized them as monotypic families (Table 1). However, he still considered these two genera close allies of *Cornus* and members of his Cornales.

Cronquist (1981), in contrast, retained a broader view of Cornaceae than Takhtajan (Table 1). Cronquist (1981) closely followed the treatment of Wangerin (1910) (Table 1), but added *Aralidium* to Cornaceae. Cronquist (1988) later added the nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*) to Cornaceae following Eyde (1988) and included all of Harms's (1898) genera except *Alangium* and *Garrya* in his Cornaceae. He argued against dividing Cornaceae into a number of small or monotypic families as done by Takhtajan.

Attempting to synthesize all available evidence, Eyde (1988) considered the Cornaceae to consist of *Cornus*, nyssoids, and mastixioids (modern *Mastixia* and its fossil allies) (Table 1). Eyde also proposed that mastixioids may be the closest relatives of *Cornus* based primarily on a single shared trait: a two-armed surface hair formed from a single cell. The delimitation of Cornaceae became even less clear with the recent addition of *Diplopanax* to Cornaceae (Eyde & Xiang, 1990). *Diplopanax*, which consists of a single species (*D. stachyanthus* Hand.-Mazz.) occurring rarely in southern China and northern Vietnam, was previously placed in Araliaceae (Handel-Mazzetti, 1933).

Not only do concepts of Cornaceae vary greatly, but there is considerable disagreement regarding the closest relatives of *Cornus*. Different lines of evidence have suggested a wide array of closest relatives for *Cornus* (Table 3). Evidence from embryology, for example, suggests that *Alangium* is the closest ally of *Cornus* (Chopra & Kaur, 1965), whereas chromosome numbers suggest that *Nyssa*, *Davidia*, *Mastixia*, and *Garrya* are also close relatives of *Cornus* (Goldblatt, 1978). Seed structure (germination valves) provides a still different picture, suggesting a close relationship among *Cornus*, *Mastixia*, *Diplopanax*, *Nyssa*, and *Davidia* (Eyde, 1963, 1988; Eyde & Xiang, 1990). Evidence from palynology, wood anatomy, serology, secondary chemistry, and fatty acid chemistry each suggests a different suite of close relatives for *Cornus* (Table 3; Bate-Smith et al., 1975; Breuer et al., 1987; Fairbrothers & Johnson, 1964; Ferguson, 1977; Ferguson & Hideux, 1980; Li & Chao, 1954).

The taxonomic complexity of Cornaceae is further compounded by the extreme polymorphism of *Cornus*. Wangerin (1910) classified the genus into seven subgenera (Table 4) using primarily the morphology of the inflorescence, bracts, and fruits.

TABLE 2. Geographic distribution and species composition of *Cornus* and putatively related genera.

| | |
|---|---|
| *Alangium* | ca. 20 spp., mostly in Asia, a few in Polynesia, New Guinea, subtropical Australia, tropical Africa, Madagascar, Comoro Islands. |
| *Aralidium* | 3 spp., Malaya. |
| *Aucuba* | 3–11 spp., eastern Himalayas to Japan. |
| *Camptotheca* | 1 sp., southwestern and south-central China. |
| *Cornus* | ca. 45 to 60 spp., mostly in eastern Asia and North America, a few in Europe, 1 in Central America, 2 in South America, and 1 in tropical Africa. |
| *Corokia* | 6 or 7 spp., South Pacific islands. |
| *Curtisia* | 2 sp., southern Africa. |
| *Davidia* | 1 sp., southwestern China and western Hupei of China. |
| *Diplopanax* | 1 sp., southern China and northern Vietnam. |
| *Garrya* | 14 spp., southwestern United States, Mexico, West Indies. |
| *Griselinia* | 6 spp., New Zealand, Chile, and Brazil. |
| *Helwingia* | 3 spp., Himalayas to Japan. |
| *Kaliphora* | 1 sp., Madagascar. |
| *Mastixia* | 13 spp., southeastern Asia and western Pacific. |
| *Melanophylla* | 9 spp., Madagascar. |
| *Nyssa* | 7 spp., eastern Asia, eastern North America, northern Mexico. |
| *Toricellia* | 2 or 3 spp., eastern Himalayas and southwestern China. |

Wangerin's view of *Cornus* has been largely followed by most modern investigators (Eyde, 1987; Ferguson, 1966; Xiang, 1987). In contrast, *Cornus* has been divided by some into as many as six genera (Table 5; Hutchinson, 1942, 1967; Pojarkova, 1950). The complex history of this problem and the nomenclatural changes involved have been reviewed by Eyde (1987) and Ferguson (1966).

Phylogenetic relationships among species groups within *Cornus* have also been debated. *Cornus* can be roughly divided into four groups: big-bracted dogwoods, dwarf dogwoods, cornelian cherries, and bractless dogwoods. Emphasizing the distribution of iridoids, Bate-Smith et al. (1975) proposed that the big-bracted dogwoods are the most primitive species of *Cornus* and the bractless dogwoods are the most advanced. This view is supported by evidence from wood anatomy (Adams, 1949; Li & Chao, 1954) and floral anatomy (Wilkinson, 1944). Dermen (1932) proposed that based on chromo-

TABLE 3. Close relatives of *Cornus* as suggested by eight different lines of morphological, anatomical, karyological, and chemical evidence.

| Characters | Suggested close relatives |
|---|---|
| Cytology | *Nyssa*, *Davidia*, *Mastixia*, and *Garrya* (Goldblatt, 1978) |
| Pollen morphology | *Curtisia*, *Mastixia*, *Nyssa*, *Davidia*, and *Camptotheca* (Eramyan, 1971; Ferguson, 1977; Ferguson & Hideux, 1980; Eyde, 1988; Reitsma, 1970) |
| Floral anatomy | *Nyssa*, *Davidia*, *Mastixia*, and *Toricellia* (Eyde, 1967, 1988) |
| Fruit morphology | *Mastixia*, *Diplopanax*, *Nyssa*, and *Davidia* (Eyde, 1963, 1988) |
| Embryology | *Alangium* (Chopra & Kaur, 1965) |
| Wood anatomy | *Corokia*, *Helwingia*, *Schefflera*, *Nyssa*, *Garrya*, *Mastixia*, *Viburnum*, and *Griselinia* (Li & Chao, 1954) |
| Secondary metabolic products | *Mastixia*, *Curtisia*, and *Davidia* (Bate-Smith et al., 1975) |
| Fatty acid chemistry | *Curtisia*, *Mastixia*, and *Corokia* (Breuer et al., 1987) |

some numbers and sizes, the cornelian cherry group is basal within *Cornus*. Eyde (1988), in contrast, proposed that the genus early diverged into two main lineages, a bracted (or red-fruited) line in which the inflorescence has basal bracts, and a bractless (or blue- or white-fruited) line in which the bracts are rudimentary or lacking. The bracted line includes the big-bracted dogwoods, dwarf dogwoods, and the cornelian cherries. Using morphological characters and evidence from fossils and embryology, Eyde proposed that the bractless dogwoods are ancestral and connect *Cornus* to the nyssoids. He classified *Cornus* into four informal subgroups without giving these groups taxonomic rank: bractless dogwoods, cornelian cherries, big-bracted dogwoods (including the Mexican disciflorous dogwoods), and dwarf dogwoods.

TABLE 4. Intrageneric treatment of *Cornus* proposed by Wangerin (1910): 50 species divided into seven subgenera. All species are woody and have bisexual flowers except those indicated.

| | |
|---|---|
| *Thelycrania* | bractless dogwoods, 36 spp. with spreading cymes. |
| *Afrocrania* | African cornelian cherry, 1 dioecious species, with four small herbaceous bracts subtending an umbel-like cyme. |
| *Macrocarpium* | cornelian cherries, 4 spp. with four herbaceous bracts subtending an umbel-like cyme. |
| *Arctocrania* | dwarf dogwoods, 2 herbaceous spp. with four petaloid bracts subtending a condensed cyme. |
| *Discocrania* | Mexican disciflorous dogwood, 2 spp. with four small, herbaceous, and early deciduous bracts subtending a capitate inflorescence. |
| *Benthamidia* | North American big-bracted dogwoods, 2 spp. with four large petaloid bracts subtending a capitate inflorescence. |
| *Benthamia* | Asian big-bracted dogwoods, 3 spp. with four large petaloid bracts subtending a capitate inflorescence which subsequently develops into a compound fruit. |

From the above review it is apparent that another experimental approach is needed to help unravel the systematic problems posed by Cornaceae. We therefore employed comparative sequencing of *rbc*L with the following objectives: (1) clarify relationships among *Cornus* and putatively related genera, and (2) elucidate evolutionary relationships among the major subgroups within *Cornus*. The advantages of *rbc*L sequencing for addressing phylogenetic questions at this level have been well reviewed (e.g., Clegg & Zurawski, 1992; Palmer et al., 1988).

## MATERIALS AND METHODS

Species included in this study represent the major subgroups of *Cornus* as well as taxa that previously have been considered closely allied with *Cornus* by at least some investigators (e.g., *Cornus alternifolia* L.f., *C. canadensis* L., *C. chinensis* Wangerin, *C. florida* L., *C. kousa* Hance, *C. mas* L., *C. obliqua* Raf., *C. oblonga* Wall., *C. officinalis* Siebold & Zucc., *C. walteri* Wangerin; *Alangium chinense* (Lour.) Harms, *Aucuba japonica* Thunb., *Camptotheca acuminata* Decne., *Corokia cotoneaster* Raoul, *Curtisia dentata* (Burm.f.) G.A.Sm., *Davidia involucrata* Baill., *Diplopanax stachyanthus* Hand.-Mazz., *Garrya elliptica* Douglas ex Lindl., *Griselinia lucida* J.G. Forst, *Helwingia japonica* (Thunb.) F. Dietr., *Mastixia caudatilimba* C.Y. Wu ex Soong, *Nyssa ogeche*

TABLE 5. Comparison of several taxonomic schemes proposed for *Cornus* sensu lato, depicting the magnitude of the discrepancies that exist.

| Strict view | | Broad view | |
|---|---|---|---|
| Pojarkova (1950) (6 genera) | Hutchinson (1967) (6 genera) | Wangerin (1910) (7 subgenera) | Ferguson (1966) (8 subgenera) |
| *Thelycrania* | *Svida* | *Thelycrania* | *Kraniopsis* |
| *Bothrocaryum* | | | *Mesomora* |
| *Afrocrania* | *Afrocrania* | *Afrocrania* | *Afrocrania* |
| *Cornus* | *Cornus* | *Macrocarpium* | *Cornus* |
| | *Cynoxylon* | *Arctocrania* | *Arctocrania* |
| *Cynoxylon* | | *Discocrania* | *Discocrania* |
| | *Dendrobenthamia* | *Benthamidia* | *Cynoxylon* |
| *Chamaepericlymenum* | *Chamaepericlymenum* | *Benthamia* | *Benthamia* |

Marsh; see Appendix of this issue). The sequence for *Cornus kousa* was provided by R. G. Olmstead (unpublished). These taxa represent the major cast of characters required for a molecular phylogenetic analysis of *Cornus* and putative relatives. It would have been desirable to include in this study several additional genera (*Kaliphora*, *Melanophylla*, *Toricellia*, and *Aralidium*) of which we could not obtain either living or recent herbarium collections due to their rarity and/or geographically restricted distributions (Table 2).

Total DNAs were isolated from leaf tissue following the method of Doyle & Doyle (1987) as modified by Soltis et al. (1991). Double-stranded *rbc*L was amplified using thermostable DNA polymerase provided by either Promega or Epicentre Technologies. Primers used for amplifications are synthetic oligonucleotides. The forward or 5′ primer (Z1) is composed of the first 30 bases of *rbc*L of *Zea mays* L. Two different reverse primers were used. The one used most often (3′*rbc*L) is that of Olmstead et al. (1992), which consists of 34 bp beginning 103 base pairs outside of the terminus of the gene in *Nicotiana*. For *Diplopanax* and *Mastixia*, however, this Z1-3′*rbc*L primer combination did not yield a product so we used an internal reverse primer, a 30-mer beginning at position 1351 of *rbc*L in *Z. mays*.

The double-stranded products subsequently were used as templates, and the forward and reverse primers used individually for single-stranded DNA amplifications. Single-stranded products were precipitated with 20% PEG/2.5M NaCl. DNA pellets were washed once each with 70% and 95% EtOH, dried, and redissolved in TE. DNA sequencing followed the dideoxy method using Sequenase 2.0 enzyme and the Sequenase 3.1 kit (U.S. Biochemical Corp.). Sequencing primers were derived from the *rbc*L sequence of *Z. mays* and kindly provided by G. Zurawski (DNAX Research Institute). Both the forward and reverse strands were sequenced for all taxa.

Twenty-one sequences were generated in this study for *Cornus* and putatively related genera. Twenty-five additional sequences from Saxifragales, Apiales, and Asteridae (Fig. 1, also see Appendix, this issue) were included in a phylogenetic analysis to determine possible alliances of *Cornus*. *Cercidiphyllum* and *Daphniphyllum* (representatives of Hamamelidae) and *Itea*, *Saxifraga*, and *Astilbe* (representatives of Rosidae) served as outgroups for this analysis because they are close to, yet basal to, the taxa included in this broad *rbc*L sequence analysis. The choice of taxa and outgroups for use in our analysis was based on the results of the large phylogenetic analysis of 499 *rbc*L sequences for seed plants (Chase et al., 1993).

For all taxa but *Diplopanax* and *Mastixia*, 1377 bp of *rbc*L sequence data were compared beginning at position 31 and ending at base pair 1407. Due to the amplification strategy required for *Diplopanax* and *Mastixia* (see above), we analyzed 1320 bp for these genera, from position 31 to 1350. All parsimony analyses were conducted with PAUP version 3.0s (Swofford, 1991) using MULPARS and TBR branch-swapping with characters specified as unordered and unweighted. To ensure that all "islands" of shortest trees were found (Maddison, 1991), 100 tree searches were performed each with a different order of taxa addition. A bootstrap analysis using 100 replicates was also conducted to obtain estimates of reliability for each monophyletic group.

## RESULTS

The phylogenetic analysis resulted in 690 most parsimonious trees that were 1,185 steps long, all in one island (Fig. 1). Two major groups can be identified in all of the most parsimonious trees. One

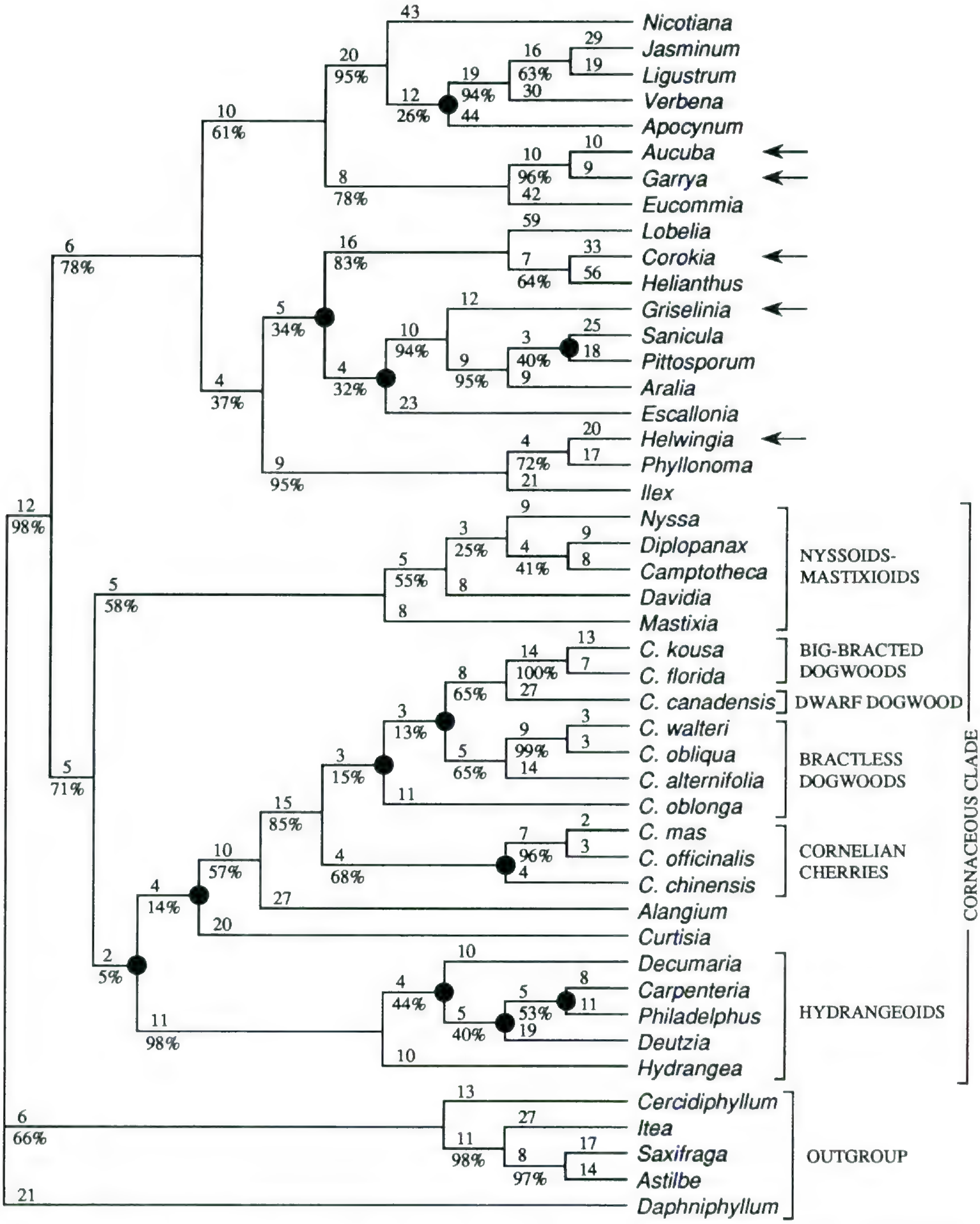


FIGURE 1. The majority-rule consensus tree including all compatible groupings constructed from 690 minimum length trees resulting from parsimony analysis of *rbc*L sequences of Cornaceae and additional taxa. This tree is one of the 690 shortest trees (length = 1,185 steps, consistency index = 0.470, retention index = 0.541). The tree is rooted using representatives from Hamamelidae (*Cercidiphyllum* and *Daphniphyllum*), and Rosidae (*Itea*, *Saxifraga*, and *Astilbe*). Numbers above lines indicate the number of nucleotide substitutions supporting each branch. Numbers below lines indicate the percentage of occurrence of each monophyletic group in the results of 100 bootstrap samples. Nodes that are not present in all 690 most parsimonious trees are indicated by black circles. Arrows indicate taxa outside the cornaceous clade that have been placed in Cornaceae by some investigators. Species of *Cornus* are abbreviated "*C.*"

of these groups comprises *Cornus*, *Alangium*, *Curtisia*, *Nyssa*, *Camptotheca*, *Davidia*, *Diplopanax*, *Mastixia*, and genera from Hydrangeaceae (*Decumaria*, *Carpenteria*, *Deutzia*, *Philadelphus*, and *Hydrangea*) (Fig. 1). This group, hereafter referred to as the "cornaceous clade," has a bootstrap value of 71% (Fig. 1). The analysis of Chase et al. (1993) similarly indicates a monophyletic group identical to the cornaceous clade. Four major lineages can be recognized within the cornaceous clade, although the bootstrap values for some are not high: (1) nyssoids (*Nyssa*, *Camptotheca*, *Davidia*)–mastixioids (*Diplopanax* and *Mastixia*) (58%), (2) *Cornus*–*Alangium* (57%), (3) *Curtisia*, and (4) hydrangeoids (*Decumaria*, *Carpenteria*, *Deutzia*, *Philadelphus*, and *Hydrangea*) (98%) (Fig. 1). The second major group contains all of the remaining taxa analyzed, including those that have been considered close relatives of *Cornus* (*Aucuba*, *Garrya*, *Helwingia*, *Griselinia*, and *Corokia*). These five taxa are not closely allied with the cornaceous clade (Fig. 1). *Griselinia* is the sister of a well-supported (bootstrap value of 95%) araliaceous group. *Corokia* is allied with Asteraceae. *Helwingia* has as its closest relative *Phyllonoma*, a genus usually placed in Escalloniaceae or treated as a distinct subfamily of Saxifragaceae sensu lato (discussed in greater detail by Morgan & Soltis, 1993). *Aucuba* and *Garrya* are close allies; both appear in a clade with *Eucommia* (Eucommiaceae: Hamamelidae). The phylogenetic positions of these five genera traditionally allied with Cornaceae are congruent with those derived from the broad analysis of Chase et al. (1993), and a detailed analysis of sequences from the Asteridae (Olmstead, unpublished).

The phylogenetic analysis of *rbc*L sequences reveals that *Cornus* is a well-supported monophyletic group (85%; Fig. 1). Four lineages can be recognized among the 10 species of *Cornus* sequenced, although these clades are not strongly supported in the bootstrap analysis: (1) big-bracted dogwoods–dwarf dogwoods (65%), (2) bractless dogwoods (65%), (3) cornelian cherries (68%), and (4) *C. oblonga*, a morphologically distinct bractless species (Fig. 1). Strongly supported lineages having bootstrap values of 96%–100% are further identified within three of these four lineages: the big-bracted dogwoods (*C. kousa* and *C. florida*), the opposite-leaved bractless species (*C. walteri* and *C. obliqua*), and two cornelian cherries (*C. mas* and *C. officinalis*) (Fig. 1). Sequence divergence among species of *Cornus* is very high. For example, *C. canadensis* differs from *C. kousa* by 54 base substitutions and *C. mas* differs from *C. canadensis* by 54 base substitutions (Fig. 1).

## Discussion

Numerous studies have demonstrated the great value of *rbc*L sequence data in reconstructing plant phylogenies (e.g., Doebley, 1990; Donoghue et al., 1992; Olmstead et al., 1992; Soltis et al., 1990; papers in this issue). The value of comparative *rbc*L sequencing for resolving phylogenetic questions in particularly troublesome groups is also illustrated by our analysis of Cornaceae. In this study, *rbc*L sequence data have (1) helped to identify an alliance composed of *Cornus* and related taxa (i.e., the cornaceous clade), (2) demonstrated that several genera traditionally allied with *Cornus* are only distantly related to this genus, and (3) suggested the presence of major lineages within the cornaceous clade and within *Cornus*.

### 1. The Cornaceous Clade

Our analysis reveals that *Cornus* is a well-supported lineage and suggests that nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*), mastixioids (*Diplopanax* and *Mastixia*), *Alangium*, *Curtisia*, and hydrangeoids are the closest relatives of *Cornus* (Fig. 1). No suite of cornaceous relatives identical to those suggested by *rbc*L sequence data has been proposed previously, and only the proposals of Eyde (1988) and Takhtajan (1980, 1987) are somewhat close to the scheme suggested by our analysis of *rbc*L sequences.

*Alangium* has been widely recognized as a monotypic family (e.g., Cronquist, 1981, 1988; Hutchinson, 1967; Takhtajan, 1980, 1987; Wangerin, 1910). Our phylogenetic analysis of *rbc*L sequence data suggests that *Alangium* may be the sister group to *Cornus*. A close relationship between these two genera is also suggested by similarities in flowers, fruits, and embryology (Chopra & Kaur, 1965; Eyde, 1988), binucleate pollen (Brewbaker, 1967), and a base chromosome number of $x = 11$. In addition, one species of *Alangium* has the distinctive two-armed hairs (but with unequal arms) characteristic of *Cornus* (see Eyde, 1988). Eyde (1988) similarly concluded that *Alangium* was a close relative of *Cornus* using the above characters.

Nyssoids differ from *Cornus* primarily in having unisexual and polygamous flowers. However, nyssoids also share a number of important characters with *Cornus*: presence of iridoids (Bate-Smith et al., 1975), similar gynoecial vasculature (Eyde, 1967), germination valves on the fruit stone (Eyde,

1988), and H-shaped thinning of the pollen aperture (Eramyan, 1971; Ferguson, 1977; Ferguson & Hideux, 1980; Reitsma, 1970). Citing these features, Eyde (1988) proposed that nyssoids share a recent common ancestor with *Cornus*. Our sequence data, therefore, agree with these morphological, anatomical, and chemical similarities in suggesting that the nyssoids are closely related to *Cornus* (Fig. 1).

Relationships among nyssoids (*Nyssa*, *Davidia*, and *Camptotheca*) have long been controversial. The three genera of nyssoids are often placed in the family Nyssaceae (Cronquist, 1981; Hutchinson, 1967; Wangerin, 1910). Fruit and seed morphology, as well as evidence from wood anatomy and fatty acid chemistry (Breuer et al., 1987; Eyde, 1963, 1988; Hohn & Meinschein, 1976; Titman, 1949), suggests a close relationship among the nyssoids. However, *Davidia* has been recognized as a monotypic family by some authors (Takhtajan, 1980, 1987). Using wood anatomy, Titman (1949) proposed that *Davidia* is the most primitive nyssoid, with *Camptotheca* derived from *Nyssa*. This proposal was supported by evidence from fatty acids (Breuer et al., 1987; Hohn & Meinschein, 1976), and data from morphological, palynological, and fossil studies (Eyde, 1963, 1988). Chen (1988) argued, however, that *Camptotheca* was only distantly related to *Nyssa* based on his embryological studies of *Camptotheca*, *Nyssa*, and *Davidia* and proposed a new monotypic family, Camptothecaceae (Chen, 1988). Serological data (Fairbrothers, 1977; Fairbrothers & Johnson, 1964), on the other hand, support the separation of *Davidia* from *Nyssa* and *Camptotheca*. Our analysis of *rbc*L sequence data suggests instead that these three genera, together with *Mastixia* and *Diplopanax*, form a monophyletic group.

*Diplopanax* was placed previously in Araliaceae by Handel-Mazzetti (1933) based on the resemblance of its flowers, without observation of fruits, to those of the araliaceous genus *Dendropanax*. This family assignment was questioned by Hoo & Tseng (1978) and Tseng (1983). They found important similarities between the fruits of *Diplopanax* and *Mastixia* and suggested that *Diplopanax* is better placed in Cornaceae. Eyde & Xiang (1990) made a direct comparison of *Diplopanax* fruits with fossil fruits of mastixioids and restated that *Diplopanax* is closely allied with *Mastixia* because both share distinctive fruitstones, two-armed hairs that are one-celled on the leaf midveins, and hooked petals. These structural features place *Diplopanax* in the genus *Mastixicarpum*, part of a woody-fruited mastixioid complex that was thought to have gone extinct four million years ago. Although *Mastixicarpum* is the older name, nomenclatural rules require that the united group take the name of its modern component, *Diplopanax*.

Our *rbc*L sequence data place *Diplopanax* in the nyssoid group and support its removal from Araliaceae where it was initially placed (Handel-Mazzetti, 1933) and has since been classified (Hoo & Tseng, 1978; Hutchinson, 1967). Although *rbc*L sequence data indicate that *Diplopanax* is a close relative of *Mastixia*, whether *Diplopanax* is most closely related to *Mastixia* (as suggested by Eyde & Xiang, 1990) is still uncertain based on *rbc*L sequences. All of our analyses show *Diplopanax* to be closest to *Camptotheca*, but this relationship is not strongly supported by the bootstrap analysis (41%) (Fig. 1). *Diplopanax* and *Camptotheca* are similar in that both genera (as well as *Mastixia*) are diplostemonous. Further assessment of possible relationships between *Diplopanax* and the nyssoid genera are not presently possible because of the lack of embryological, chemical, and anatomical evidence for *Diplopanax*, a result of the geographic isolation and rarity of the genus.

*Mastixia* has been assigned to a diverse array of families (e.g., Caprifoliaceae, Nyssaceae, Aquifoliaceae, Araliaceae, Icacinaceae, and Cornaceae; Matthew, 1976). Phylogenetic analysis of *rbc*L sequence data reveals that *Mastixia* is a member of the cornaceous clade. A number of lines of evidence (Table 3) suggest a close relationship between *Mastixia* and *Cornus*. However, based on *rbc*L sequences, *Mastixia* does not appear to be the sister of *Cornus* as suggested by Eyde (1988) but is more closely related to the nyssoids instead (Fig. 1). Thus, the two-armed surface hairs shared by *Mastixia*, *Diplopanax*, and *Cornus* (Eyde, 1988) may actually have evolved independently in each of these genera.

*Curtisia*, comprising two species endemic to South Africa, clearly is a member of the cornaceous clade in these analyses of *rbc*L sequences. Similar chemical patterns were observed in *Cornus* and *Curtisia* by Bate-Smith et al. (1975), adding further support for a close relationship between the two genera. *Curtisia* also has been linked with *Mastixia* based on chromosomal (Goldblatt, 1978) and palynological data (Ferguson, 1977; Ferguson & Hideux, 1980; Hideux & Ferguson, 1976). In contrast, Eyde (1988) did not consider *Curtisia* to be a close ally of *Cornus*, *Mastixia*, and nyssoids (his Cornaceae) because of its small pollen grains

and distinctive fruit-stone vascular bundles. *Curtisia* generally is placed in Cornaceae as a separate subfamily (Harms, 1898; Takhtajan, 1980; Thorne, 1983; Wangerin, 1910) or recognized as a monotypic family placed close to Cornaceae (Takhtajan, 1987; Thorne, 1992). Both of these views are concordant with *rbc*L sequence data.

The relationships of hydrangeoids have long been controversial (see review of this topic by Morgan & Soltis, 1993). Our analysis of *rbc*L sequences clearly supports their position as close relatives of *Cornus*, *Alangium*, *Curtisia*, nyssoids, and mastixioids, as suggested previously by Breuer et al. (1987), Takhtajan (1987), Philipson (1977), and Krach (1977) based on other lines of evidence. Hydrangeoids are similar to other members of the cornaceous clade in general flower structure: flowers 4–5-merous with an epigynous disk, calyx tube adnate to the ovary, petals free, ovary inferior (sometimes incompletely inferior as in *Hydrangea* or superior as in *Carpenteria*) with 2–5 locules, and ovules usually pendulous. In addition, both hydrangeoids and other members of the cornaceous clade produce iridoids. Several features, however, clearly separate the hydrangeoids from other members of the cornaceous clade. Hydrangeoids possess numerous ovules per locule, capsular fruits, and central bundles in the gynoecial vasculature. All other members of the cornaceous clade, in contrast, have a solitary ovule in each locule, typically bear drupes (*Camptotheca* has subsamaroid fruits), and lack central bundles in the gynoecial vasculature. Furthermore, hydrangeoids have unitegmic tenuinucellate ovules whereas nearly all the other members of the cornaceous clade (excluding *Curtisia* for which ovule type is unknown) have unitegmic crassinucellate ovules (Philipson, 1977). An exception is found in the bracted species of *Cornus*, which like the hydrangeoids have unitegmic tenuinucellate ovules (Erdelska, 1986; Eyde, 1988).

Although analysis of *rbc*L sequences has identified a well-supported cornaceous clade comprising four major lineages, relationships among these four major lineages are not resolved. To clarify more fully relationships within the cornaceous clade, sequences of more rapidly evolving nuclear or chloroplast genes will be required.

## 2. DISTANT RELATIVES OF CORNACEAE

Not only do *rbc*L sequence data indicate the presence of a cornaceous clade, these data also reveal that *Aucuba*, *Garrya*, *Corokia*, *Griselinia*, and *Helwingia*, all traditionally placed in Cornaceae, are not closely related to *Cornus* or to other members of the cornaceous clade (Fig. 1). Our findings are consistent with the broad phylogenetic analysis (Chase et al., 1993), which similarly indicates that these five genera are distantly related to the cornaceous clade. These genera have been placed in Cornaceae or Cornales by different taxonomists because of their tree or shrub form, vessel-segments usually with scalariform perforations, 3–5-merous and inconspicuous flowers, partially united sepals, separate petals, epigynous discs, inferior ovaries, solitary ovules per locule, and mostly drupaceous fruits. Each of these genera is discussed individually below.

*Aucuba* was placed in Cornaceae by Harms (1898), Wangerin (1910), and Cronquist (1981) and considered a close relative of Cornaceae by Takhtajan (1980, 1987). Our *rbc*L sequence analysis reveals, however, a distant relationship between *Aucuba* and the cornaceous clade. The distant relationship of *Aucuba* to the cornaceous clade is also supported by its distinctive wood structure and pollen morphology (Adams, 1949; Ferguson & Hideux, 1980). The closest relative of *Aucuba*, based on *rbc*L sequence data, is *Garrya*, a genus of 15 species in North America and the West Indies. *Garrya* has also been placed in Cornaceae (Harms, 1898) or recognized (as Garryaceae) as a close relative of Cornaceae (Cronquist, 1988; Hutchinson, 1967, 1969; Takhtajan, 1987; Thorne, 1983, 1992). The close affinity between *Aucuba* and *Garrya* suggested by sequence data is also supported by similarities in gynoecial vasculature (Eyde, 1964), phytochemistry (Bate-Smith et al., 1975), and fatty acids present in seed oils (Breuer et al., 1987).

*Corokia* is also far removed phylogenetically from *Cornus* in our analysis of *rbc*L sequences. Although *Corokia* traditionally has been placed in Cornaceae, more recently it has been considered closely related to *Argophyllum* (Escalloniaceae) based on pollen morphology and wood and floral anatomy (Eyde, 1988; Takhtajan, 1987). However, *rbc*L sequence data also reveal a distinct relationship between *Corokia* and *Escallonia*; an *rbc*L sequence is not available for *Argophyllum*.

Most treatments have placed *Griselinia* in Cornaceae (Cronquist, 1988; Harms, 1898; Hutchinson, 1967; Wangerin, 1910). It was, however, recognized as a monotypic family in Cornales by Takhtajan (1980), and later moved to his Hydrangeales (Takhtajan, 1987). Close affinities among *Griselinia*, *Aucuba*, and *Garrya* were proposed by Eyde (1964) based on gynoecial vascu-

lature. Phytochemical evidence also supports these relationships (Breuer et al., 1987). However, *rbc*L sequence data place *Griselinia* in a basal position in the araliaceous group, phylogenetically distant from *Aucuba* and *Garrya* (Fig. 1).

*Helwingia* was placed in Cornaceae by Harms (1898), Wangerin (1910) and Cronquist (1981). Our analysis of *rbc*L sequences reveals, however, that *Helwingia* is well outside the cornaceous clade. A distant relationship between *Helwingia* and *Cornus* is also supported by phytochemical data, as well as floral characters (Bate-Smith et al., 1975; Eyde, 1967), and both Adams (1949) and Eyde (1988) suggested that *Helwingia* be removed from Cornaceae. In our analyses, the genus is phylogenetically closest to *Phyllonoma*, a traditional member of Saxifragaceae sensu lato. *Phyllonoma* is similar to *Helwingia* in that both have flowers borne on the leaf blades. Although the two genera do share this rare characteristic, no previous authors have suggested a close relationship between *Helwingia* and *Phyllonoma* (see detailed discussion of this topic by Morgan & Soltis, 1993).

## 3. PHYLOGENETIC RELATIONSHIPS WITHIN *CORNUS*

The large amount of *rbc*L sequence divergence among species of *Cornus* is somewhat surprising given the conservative rate of evolution of *rbc*L. With this large amount of sequence divergence, our results demonstrate that *rbc*L sequence data can sometimes be used to study intrageneric relationships, as discussed below.

Varying schemes of intrageneric relationships have been proposed for *Cornus*, reflecting different hypotheses of morphological evolution and different emphases on available characters (Tables 4, 5). The major argument concerns the relative advancement within the genus of the bracted versus the bractless dogwoods. Our phylogenetic analysis of *rbc*L sequence data reveals four lineages: *C. oblonga*, big-bracted dogwoods—dwarf dogwoods, cornelian cherries, and bractless dogwoods. The latter three clades were also recognized in analyses of morphological characters (Eyde, 1988) and chloroplast DNA restriction site mutations (Brunsfeld et al., 1991; Xiang et al., 1991); insufficient material of *C. oblonga* was available for inclusion of this species in the cpDNA restriction site study. However, relationships among these four lineages are incompletely resolved by *rbc*L sequences (Fig. 1). The *rbc*L sequence analysis indicates that *C. oblonga*, a bractless species found in the eastern Himalayas and southwestern China, is a lineage distinct from cornelian cherries, the remaining bractless species, and the big-bracted dogwoods–dwarf dogwoods (Fig. 1). Several morphological, embryological, and anatomical features similarly suggest the distinctiveness of *C. oblonga* (Adams, 1949; Chopra & Kaur, 1965; Zhu, 1984). This species commonly has been viewed as the most primitive species of *Cornus*, and the hypothetical ancestral dogwoods were reconstructed based largely on its morphological characters (Eyde, 1988; Rickett 1950). Although *rbc*L sequence data do not suggest a basal position for *C. oblonga* in *Cornus*, sequence data do agree with other evidence in suggesting an isolated phylogenetic position of this species in the genus. However, the exact phylogenetic position of *C. oblonga* awaits the sequence analysis of more rapidly evolving chloroplast genes, such as ORFK.

In summary, our analysis of *rbc*L sequences has (1) identified a cornaceous clade that includes *Cornus*, *Alangium*, *Curtisia*, *Nyssa*, *Camptotheca*, *Davidia*, *Diplopanax*, *Mastixia*, and genera from Hydrangeaceae (*Decumaria*, *Carpenteria*, *Deutzia*, *Philadelphus*, and *Hydrangea*); (2) revealed that several genera previously placed in Cornaceae (e.g., *Aucuba*, *Garrya*, *Corokia*, *Griselinia*, and *Helwingia*) are only distantly related to *Cornus*; (3) identified four major lineages within the cornaceous clade and suggested four major lineages within *Cornus*. Other putative relatives of *Cornus*, such as *Toricellia*, *Aralidium*, *Melanophylla*, and *Kaliphora*, may ultimately be considered part of the cornaceous clade if material becomes available for analysis of *rbc*L.

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# SYSTEMATICS OF THE ERICACEAE, EMPETRACEAE, EPACRIDACEAE AND RELATED TAXA BASED UPON *rbc*L SEQUENCE DATA[1]

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ABSTRACT

The Ericaceae, Epacridaceae, and Empetraceae are usually recognized as closely related families of woody plants that share a preference for acidic soils, anthers that invert in development, and the presence of endosperm haustoria, among other characteristics. The Empetraceae are recognized as distinctive because of their often unisexual and wind-pollinated flowers. Epacridaceae are distinguished from Ericaceae by anthers that open by slits rather than pores and a primarily Australian distribution. Phylogenetic relationships of these related families are investigated using nucleotide sequences of the plastid gene *rbc*L. Parsimony analyses indicate a monophyletic, broadly defined Ericaceae that includes Empetraceae and Epacridaceae.

The Ericaceae are acid-loving woody plants found throughout the world but with major centers of diversity in the Himalayas, tropical Asia, montane South and Central America, and southern Africa. Traditionally, this family has been closely associated with two other woody plant families that also prefer acidic habitats: Epacridaceae (primarily Australian) and Empetraceae (amphitropical). These three families share morphological, developmental, ecological, and embryological features that have led almost all recent workers to consider them closely related (e.g., Ericales sensu Cronquist, 1981). These characteristics include the presence of endosperm haustoria at both the chalazal and micropylar ends of the embryo and anthers that invert in development (see Judd & Kron, 1993). The Empetraceae comprise three genera (*Ceratiola, Corema, Empetrum*) of predominantly anemophilous plants with reduced, often unisexual flowers. *Ceratiola* and *Corema* occur in the Northern Hemisphere primarily along both sides of the Atlantic, whereas *Empetrum* exhibits a bipolar distribution. The Epacridaceae are a much larger family almost entirely restricted to Australia, although some species occur in southern South America, New Caledonia, Indomalaysia, and New Zealand. Morphologically Epacridaceae show much variability, and there are no characters that consistently distinguish all members of this family from members of the Ericaceae (Judd & Kron, 1993; D. Morrison, pers. comm.). For example, the anthers of the Epacridaceae dehisce by slits rather than pores, the latter considered typical of the Ericaceae. However, several members of the Ericaceae have anthers that dehisce by slits or slitlike pores. Traditionally, the Epacridaceae have been considered the Australian correlates of the Ericaceae (Cronquist, 1981).

The Ericaceae (in the broad sense) are a large, extremely diverse, and essentially cosmopolitan family characterized by release of pollen in tetrads and/or sympetalous urceolate or campanulate corollas (Judd & Kron, 1993). Most members of the family are photosynthetic, but Cronquist (1981) segregated the Pyrolaceae and Monotropaceae out of the Ericaceae because of the following tendencies: reduction from shrubs to herbs, gradually increasing mycoparasitism, gradual loss of chlorophyll, and choripetaly.

This study is an investigation of phylogenetic relationships among the Ericaceae, Empetraceae, and Epacridaceae. The general position of the Er-

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TABLE 1. Current classification of the taxa (listed alphabetically by order) represented in the analysis of *rbc*L sequence data of Ericaceae, Empetraceae, and Epacridaceae. Classification of Ericaceae is based on Stevens (1971). Classification of all other taxa is based on Cronquist (1981). Asterisks indicate taxa that functioned as outgroups in this study.

| Order | Family | Subfamily | Representative taxa |
|---|---|---|---|
| Diapensiales | Diapensiaceae | | *Diapensia** |
| Ebenales | Ebenaceae | | *Diospyros** |
| | Sapotaceae | | *Chrysophylium** |
| | | | *Manilkara** |
| | Styraceae | | *Styrax** |
| | Symplocaceae | | *Symplocus** |
| Ericales | Clethraceae | | *Clethra** |
| | Cyrillaceae | | *Cyrilla** |
| | Empetraceae | | *Ceratiola* |
| | Epacridaceae | | *Cyathodes, Dracophyllum, Epacris, Leucopogon, Pentachondra* |
| Ericales | Ericaceae | Ericoideae | *Calluna, Erica* |
| | | Pyroloideae | *Pyrola* |
| | | Rhododendroideae | *Befaria, Daboecia, Elliottia, Leiophyllum, Rhododendron* |
| | | Vaccinioideae | *Arbutus, Arctostaphylos, Cassiope, Chamaedaphne, Enkianthus, Gaultheria, Leucothoë, Vaccinium, Zenobia* |
| Geraniales | Balsaminaceae | | *Impatiens** |
| Polemoniales | Polemoniaceae | | *Polemonium** |
| Primulales | Myrsinaceae | | *Ardisia** |
| | Primulaceae | | *Anagallis** |
| | Theophrastaceae | | *Clavija** |
| Rosales | Byblidaceae | | *Roridula** |
| Sarraceniales | Sarraceniaceae | | *Sarracenia** |
| Theales | Actinidiaceae | | *Actinidia** |
| | Theaceae | | *Camellia** |
| Violales | Fouquieriaceae | | *Fouquieria** |

icales (Cronquist, 1981) within the flowering plants is addressed in Chase et al. (1993) and Olmstead et al. (1993). Because of the morphological diversity and the difficulty of determining homologous structures among members of the Ericaceae, Empetraceae, and Epacridaceae, a parsimony analysis of nucleotide sequences of *rbc*L (ribulose-1, 5-bisphosphate carboxylase oxygenase, large subunit) was performed. Although the problem of homoplasy is certainly not resolved with the use of sequence data in phylogenetic analysis (cf. Albert et al., 1993), the chance that patterns of homoplasy would have similar distributions in both morphological and *rbc*L sequence data is negligible.

## MATERIALS AND METHODS

The 17 genera (including *Pyrola*) chosen for study (Table 1) represent the range of morphological diversity of the Ericaceae for an initial approximation of the limits of the family. Many of these taxa were also included in a cladistic analysis of morphological characters (Judd & Kron, 1993). *Ceratiola* (Empetraceae) and five genera representing most of the major lineages of Epacridaceae (D. Morrison, pers. comm.) were included. *Cyrilla* (Cyrillaceae) and *Clethra* (Clethraceae) were also included because they are often considered closely related to the ericads (Cronquist, 1981). Whereas the focus of this study is the circumscription of the Ericaceae, representatives of several families within the subclass Dilleniidae (Cronquist, 1981) were included in a broad analysis (see Chase et al., 1993) to provide a context for previously hypothesized relationships with the ericalean taxa (e.g., Cronquist, 1981; Dahlgren, 1983; Hufford, 1992; Takhtajan, 1980; Thorne, 1983, 1992). These taxa have often been considered as either related

or ancestral to the Ericaceae. The sampling of "dilleniid" taxa is not complete. Thus assessment of relationships outside the Ericaceae s.l. is tentative (see the Appendix at the end of this issue for a list of vouchers).

Total DNA was extracted from fresh leaves via the modified CTAB procedure (Doyle & Doyle, 1987). The *rbc*L gene was amplified using engineered primers, cloned, and then sequenced using the standard dideoxy method (see Olmstead et al., 1993). Because of the size-conserved nature of *rbc*L, visual alignment of the sequences was easily performed. The sequences were analyzed with PAUP version 3.0s (Swofford, 1991) using heuristic search methods (see methods in Chase et al., 1993). This provided a clade as a starting point for the following analyses.

In the broad analysis, 41 of the "ericalean" and "dilleniid" taxa sampled appear in a single clade (length of this portion of the tree = 1,169 steps; see asterid III, figs. 13A, B in Chase et al., 1993) sister to the lineage that contains traditional "asterid" taxa (Cronquist, 1981). These 41 taxa (Fig. 1) were therefore used in subsequent "local" analyses. The sequences of these taxa were analyzed as a group, using PAUP 3.0s (Swofford, 1991). Eighteen of the 41 taxa (Table 1) in this clade functioned as outgroups (Maddison et al., 1984) for the Ericaceae s.l. Trees were arranged with the Primulales clade sister to the remaining taxa (Fig. 1). Two types of analyses were performed: (1) Ten replicates of random sequence addition were used to find the shortest tree (TBR, MULPARS, STEEPEST DESCENT, all characters and character states weighted equally). To select a tree to illustrate from among the numerous most parsimonious trees obtained, the weighting criterion of Albert et al. (1993) was applied. (2) A search (TBR, MULPARS) was made for trees up to and including five steps longer than the most parsimonious trees found in the first analysis. Consensus trees were constructed using the FILTER option at each step. In this analysis the following outlying taxa were removed to decrease the time involved in the search for longer trees: *Anagallis*, *Ardisia*, *Chrysophyllum*, *Clavija*, *Diapensia*, *Diospyros*, *Fouquieria*, *Impatiens*, *Polemonium*, *Styrax*, and *Symplocus*. This allowed us to assess the relative robustness of the clades within the Ericaceae obtained with maximum parsimony (cf. Bremer, 1988; Novacek, 1991). Thus, clades that collapse in trees one step longer (i.e., one step less parsimonious) are less robust than clades that remain intact in trees up to five steps longer than maximum parsimony. (This is the "decay index" of Mishler et al., 1991.) We realize that ten replicates may not reveal all islands of maximum parsimony (Maddison, 1991). However, in the decay analysis branch swapping was performed on all trees up to five steps less parsimonious, giving us greater confidence in the maximum parsimony of the initial analysis.

## Results

In the "local" analysis we performed on the 41 "ericalean" taxa, 85 trees of 1,166 steps were found with a retention index (R.I.) of 0.603. The application of the weighting criterion of Albert et al. (1993) to the 85 most parsimonious trees selected two of these trees as most parsimonious. These two trees differed only by the position of *Diospyros* (Ebenaceae). In one tree *Diospyros* is sister to the Primulales, in the second tree *Diospyros* is sister to the *Diapensia* (Diapensiaceae) *Polemonium* (Polemoniaceae) clade. Since these two trees are so similar only one is shown (Fig. 1). Decay analysis indicated that all relationships outside of the Ericaceae s.l. are weakly supported and decay at one step less parsimonious (Fig. 2).

The Ericaceae are monophyletic if Empetraceae, Epacridaceae, and Pyrolaceae are included. We will hereafter refer to this clade as Ericaceae s.l. The decay index for the branch leading to the Ericaceae s.l. indicates that the branch collapses in trees only two steps longer, indicating that there are few unique synapomorphies for the Ericaceae s.l. in the *rbc*L sequence data. This result agrees with the morphological study (Judd & Kron, 1993), where nearly all of the synapomorphies for the family show homoplasy within the family. Within the Ericaceae s.l. the currently recognized subfamilies (Stevens, 1971) Rhododendroideae and Vaccinioideae are paraphyletic. The Ericoideae are derived out of some of the "rhododendroid" taxa, and *Ceratiola* (Empetraceae) is nested within this clade. The Epacridaceae are monophyletic but are nested within the Ericaceae and are sister to some of the "vaccinioid" taxa. *Enkianthus* is the sister to the rest of the Ericaceae.

In the local analysis of the 41 "ericalean" + "dilleniid" taxa the Primulales (Cronquist, 1981) appear monophyletic with the *Clavija* (Theophrastaceae) sister to *Ardisia* (Myrsinaceae) and *Anagallis* (Primulaceae), and this clade is retained in trees one step longer (Fig. 2). The Ebenales (Table 1) are not monophyletic in this analysis. The probable paraphyletic nature of this order has already been noted by Dahlgren (1975) because of its embryological and chemical heterogeneity.

FIGURE 1. One of the 85 maximum parsimony trees (length = 1,166; C.I. (consistency index) = 0.520; R.I. (retention index) = 0.603) favored by the weighting criteria of Albert et al. (1993). Underlined taxa represent the Ericaceae s.l. This tree is arranged with the Primulales sister to all others in accord with the general results of Chase et al. (1993).

In all of the most parsimonious trees, members of the Ericaceae, Empetraceae, Epacridaceae, and Pyrolaceae form a clade. *Ceratiola* is nested within some members of subfamily Rhododendroideae (Stevens, 1971) of the Ericaceae.

## DISCUSSION

That Empetraceae may be derived from within the Ericaceae has been suggested by Moore et al. (1970) and Takhtajan (1969). Takhtajan (1969) postulated a close relationship of Empetraceae with Rhododendroideae. Harborne (1969) and Moore et al. (1970) showed that several members of the Ericaceae (e.g., *Rhododendron* and *Erica*), as well as *Ceratiola*, *Corema conradii* (Torrey) Torrey and *Empetrum* possess the rare yellow flavonol, gossypetin 3-galactoside. Thus, this chemical feature appears to unite these taxa. Rhododendroideae (Stevens, 1971) are paraphyletic, but the relationships among the members of this clade and those of the "ericoid" taxa (*Calluna* and *Erica*) are not resolved at maximum parsimony (Fig. 2). However, in at least some of the trees (Fig. 1) *Calluna* and

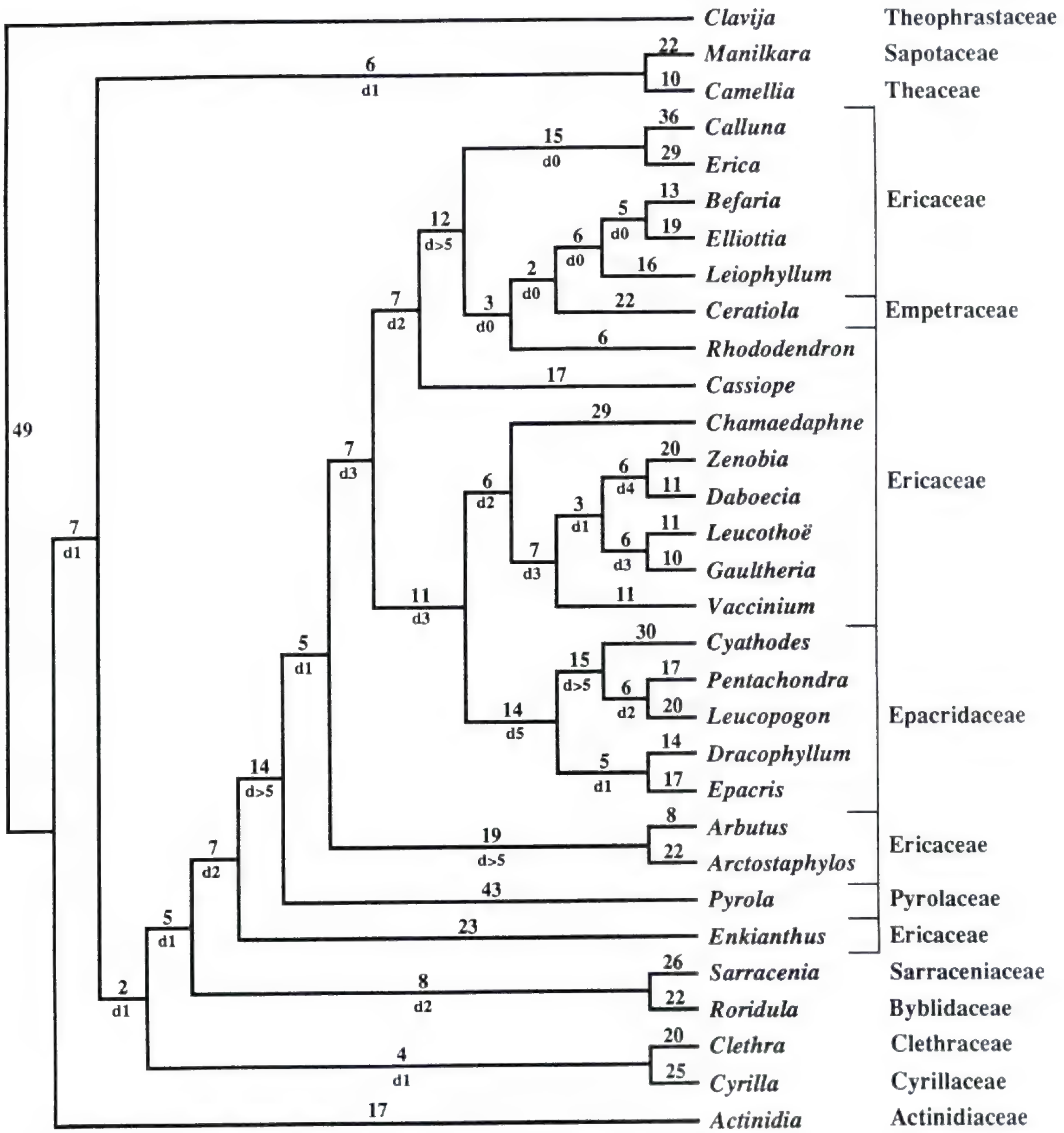


FIGURE 2. Decay of parsimony of the Ericaceae s.l. (Some outgroup taxa present in Fig. 1 were removed to reduce analysis complexity and time.) Numbers above branches are Fitch (unordered) lengths optimized with ACCTRAN of PAUP 3.0s. Numbers below branches are the decay indices or the number of steps less parsimonious at which the branch becomes a polytomy in the strict consensus tree of all trees at that length. A decay index of "d0" indicates that the branch is not present in the strict consensus tree of the 85 maximum parsimony trees; "d1" indicates that the branch is absent in the strict consensus tree of trees at maximum parsimony plus one step, etc.

*Erica* form a clade sister to the "rhododendroid" clade. This topology suggests that the "ericoid" type of leaf morphology found in *Calluna*, *Erica*, and *Cassiope* may be ancestral to the flat leaves of the "rhododendroid" taxa (Stevens, 1970). Within this clade there is also the change from gamopetalous corollas (*Cassiope*, *Calluna*, *Erica*, *Rhododendron*) to choripetalous corollas (*Ceratiola*, *Leiophyllum*, *Elliottia*, *Befaria*). This differs from the traditional view of choripetaly as the ancestral condition within the Ericaceae.

The "epacrids" are monophyletic in this analysis and are in the same clade as the "vaccinioid" taxa and *Chamaedaphne*. The "epacrid" clade is more robust (with a decay index of 5, Fig. 2) than the clade containing "vaccinioid" taxa (decay index of 3, Fig. 2). More sampling of taxa traditionally included in tribes Andromedeae and Vaccineae

(Vaccinioideae) is necessary before their relationships can be confidently evaluated.

*Arbutus* and *Arctostaphylos* (tribe Arbuteae, Vaccinioideae, Stevens, 1971) form a monophyletic group that branches before the clade leading to the bulk of the ericads. *Pyrola* is sister to the Arbuteae clade plus the above ericads. However, the relationships of *Pyrola* and Arbuteae (represented by *Arbutus* and *Arctostaphylos*) to the rest of the Ericaceae (except *Enkianthus*) are not robust in this analysis as the branch collapses in trees one step longer than maximum parsimony (Fig. 2). However, the branch leading to *Pyrola* plus the above noted ericads is well supported (decay index of >5 steps), indicating that *Pyrola* should not be recognized as a distinct family (see Judd & Kron, 1993, for supporting morphological evidence). Even though it appears that the achlorophyllous *Monotropa* lacks *rbc*L (repeated attempts to amplify the gene were not successful, see also Wolfe et al., 1992, for another achlorophyllous plant without a functional *rbc*L gene), this mycoparasitic taxon and its relatives should also be included (along with *Pyrola*, *Chimaphila*, etc.) in a broadly defined Ericaceae (Judd & Kron, 1993).

*Enkianthus* is sister to the rest of the Ericaceae (Fig. 1). This was also found in the shortest tree of Judd & Kron (1993) and A. Anderberg (pers. comm.), in studies based primarily on morphology. *Enkianthus* has been considered relatively isolated due to its combination of gamopetalous campanulate corolla, anthers opening by slits rather than pores, and pollen shed in monads rather than the tetrads characteristic of Ericaceae (Stevens, 1971). However, such a distinctive phylogenetic position has not been suggested previously. The position of *Enkianthus* as sister to the remaining Ericaceae suggests that the interpretation of a corolla with free petals as primitive (Abbott, 1936; Camp, 1941; Copeland, 1943; Stevens, 1971; Wood, 1961) within the family needs reevaluation. In fact, careful morphological studies (Copeland, 1943; Leins, 1964) show that at least in the case of members of *Rhododendron* subsect. *Ledum* (Kron & Judd, 1990), the corolla is actually slightly fused at the base early in development. The choripetalous condition may be derived within the Ericaceae in genera such as *Befaria* and *Leiophyllum*, in which the petals appear to be truly separate. However, since the sister clade to the Ericaceae s.l. may be choripetalous, it is possible that gamopetaly in *Enkianthus* is autapomorphic.

Whereas the general results obtained in this study (i.e., the inclusion of Empetraceae, Epacridaceae, and Pyrolaceae in a broadly defined Ericaceae) are supported by a cladistic analysis of morphological characters (Judd & Kron, 1993), the positions of *Cyrilla* and *Clethra* in the molecular analysis (Fig. 1) differ from those revealed in the morphological analysis. This is surprising because a close relationship of *Clethra* (Clethraceae) and *Cyrilla* (Cyrillaceae) to the Ericaceae appears to be well supported by morphology. These two genera have been included within the order Ericales by some (Cronquist, 1981; Dahlgren, 1983), although Thorne (1992) placed them in his Theales. In the morphological analysis of Judd & Kron (1993), *Actinidia* is sister to *Cyrilla* + *Clethra* + Ericaceae s.l. These taxa share the presence of an apical depression in the ovary and anthers that invert in development (modified in *Cyrilla*). In the molecular trees, the relative positions of *Actinidia*, *Cyrilla*, and *Clethra* may be resolved more fully upon inclusion of other representatives of the Cyrillaceae (*Cliftonia*, *Purdeaea*). Anderberg's (1992) cladistic study of the relationships of the Ericales to other "higher" dicots indicated Cyrillaceae and Clethraceae as branching before Roridulaceae, which is sister to Epacridaceae + Pyrolaceae + Ericaceae + Monotropaceae. These results also indicate a closer relationship of Cyrillaceae and Clethraceae to the Ericaceae s.l. than do the molecular data. However, neither the Anderberg (1992) nor the Judd & Kron (1993) studies included members of the Ebenales (sensu Cronquist, 1981) in their analyses.

## Summary

Sampling of taxa presents a major problem in molecular studies (Olmstead et al., 1993; Chase et al., 1993), and when taxa are sampled superficially spurious results are possible. We advocate and maintain a fair degree of suspicion concerning these results in two weakly supported portions of the topology and believe that increased sampling is likely to alter the estimates of relationships. One of these is the group identified as sister to Ericaceae s.l., in which significant divergence from other studies occurs (discussed above). The other area is within the Ericaceae (*Pyrola* and *Arbutus* + *Arctostaphylos*); we would expect weakly supported branches to be altered when a more even sampling is obtained. The strong internal support and congruence with results of other studies (Judd & Kron, 1993) for the positions of the segregate families (Empetraceae, Epacridaceae) make it unlikely that the general conclusions of this study will change as taxon sampling improves.

A monophyletic Ericaceae includes Empetra-

ceae, Epacridaceae, and Pyrolaceae (formally outlined in Judd & Kron, 1993). These conclusions are congruent with parsimony analysis of morphological data (Judd & Kron, 1993), which also indicates the inclusion of Monotropaceae in Ericaceae (cf. Anderberg, 1992). The agreement of these studies lends increased support to recognizing a more broadly defined Ericaceae.

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# INTERFAMILIAL RELATIONSHIPS OF THE ASTERACEAE: INSIGHTS FROM *rbc*L SEQUENCE VARIATION[1]

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## ABSTRACT

Nucleotide sequences of the chloroplast gene *rbc*L were analyzed to examine relationships among the large, distinctive family Asteraceae and eight putatively closely related families. Phylogenetic analysis of a total of 24 sequences of *rbc*L identified a lineage consisting of two families, the Goodeniaceae and Calyceraceae, as the sister group to the Asteraceae. In addition, a strongly supported major monophyletic clade consisting of Asteraceae, Goodeniaceae, Calyceraceae, *Corokia* (Cornaceae sensu Cronquist), Menyanthaceae, Lobeliaceae, and Campanulaceae was found. These results clearly distance from the Asteraceae certain groups previously considered closely related; moreover, the results support alternative hypotheses of affinity that were based upon floral and inflorescence morphology, biogeography, pollen morphology, chemistry, and pollen-presentation mechanisms.

The angiosperm family Asteraceae has long been recognized as one of the large, "natural" families with well-established limits defined by several specialized floral characteristics and distinctive secondary chemistry. Many recent studies have illuminated numerous phylogenetic controversies within the family (Bremer, 1987; Bremer et al., 1992; Jansen et al., 1990, 1991a, b; Jansen & Palmer, 1987a, b, 1988; Karis et al., 1992; Keeley & Jansen, 1991; Kim et al., 1992; Watson et al., 1991). However, relationships among the Asteraceae and other families have remained obscure, due to considerable parallel and convergent evolution of conventional characters used to infer affinities, lack of recent studies employing modern methods of phylogenetic analysis, and substantial confusion as to relationships among the various families within the subclass Asteridae itself (but see Olmstead et al., 1992).

At least 12 families have been proposed as closest relatives of the Asteraceae based on a variety of traditional taxonomic characters. Although Hutchinson (1969) noted the superficial similarity of the inflorescence of the Dipsacales (Caprifoliaceae, Valerianaceae, and Dipsacaceae) to that of the Asteraceae, he suggested convergence as the basis for this and identified the Campanulales (Campanulaceae and Lobeliaceae) as the closest relative. Aspects of the distinctive chemistry of the Asteraceae (e.g., alkaloids, polyacetylenes, terpenes, inulin for carbohydrate storage) have been noted in several members of the Campanulales (Campanulaceae, Lobeliaceae, Goodeniaceae, Stylidiaceae), while other chemical evidence has pointed to the Apiaceae and Araliaceae (Hegnauer, 1964, 1977). Cronquist (1955) advocated the Rubiales as closest relatives of the Asteraceae (grouped with the Gentianales in the system of Takhtajan, 1980), but also acknowledged strong similarities in floral and inflorescence morphology between the Asteraceae and the Calyceraceae (as did Takhtajan, 1980). An association with the Calyceraceae is also supported by biogeography and capitular structure (Turner, 1977) and pollen morphology (Skvarla et al., 1977). Others (reviewed in Skvarla et al., 1977) have noted a palynological resemblance of Valerianaceae, Goodeniaceae and Brunoniaceae to Asteraceae. In a morphological cladistic study of tribal relationships within the Asteraceae, stylar morphology, chemical characters, and pollen-presen-

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tation mechanism were identified by Bremer (1987) as potential synapomorphies linking the Lobeliaceae and Asteraceae. Finally, strong similarities to the highly specialized secondary pollen-presentation mechanism of the Asteraceae have been documented in Goodeniaceae, Brunoniaceae, Campanulaceae, and Lobeliaceae (Leins & Erbar, 1990). As noted in many of the above attempts to resolve this controversy, most of the morphological or chemical characters that support a particular hypothesis of ancestry are often also found in several related groups, and some must certainly be the product of parallel evolution.

Several of the recent molecular advances in elucidating phylogenetic relationships within the family have employed restriction site analysis of chloroplast DNA. However, this approach is generally unsuitable at the interfamilial level because the homology of site changes becomes doubtful due to increased levels of both nucleotide sequence divergence (causing multiple "hits" within restriction sites) and length variation causing problems in alignment of sites (Downie & Palmer, 1992b; Palmer et al., 1988). At higher taxonomic levels, restriction site analysis of only the more conserved inverted repeat region of chloroplast DNA may be used to circumvent these problems (e.g., Downie & Palmer, 1992a), but fewer characters are generated than in whole genome surveys. DNA sequence analysis of the slowly evolving chloroplast gene *rbc*L and nuclear rRNA genes has proven highly effective in resolving higher-level relationships in plants (Chase et al., 1993; Hamby & Zimmer, 1992; Palmer et al., 1988; Ritland & Clegg, 1987; Zurawski & Clegg, 1987). In particular, recent studies by a number of researchers employing comparative sequencing of the chloroplast gene encoding the large subunit of the photosynthetic enzyme ribulose-1,5-bisphosphate carboxylase (*rbc*L) indicate an appropriate size and rate of evolution for providing a sufficient number of characters for phylogenetic studies at the familial and ordinal levels (Donoghue et al., 1992; Kim et al., 1992; Olmstead et al., 1992; Soltis et al., 1990). In this paper we analyze nucleotide sequences for *rbc*L from representatives of the Asteraceae and eight putatively related families to determine evolutionary relationships among the families and identify the sister group of the Asteraceae.

## Materials and Methods

New *rbc*L sequences were determined for six taxa in the Asteraceae and eight representatives of putatively closely related families in the subclass Asteridae. For these sequences, fresh leaf material obtained either from the field or seedlings was used to isolate DNA as purified chloroplast DNA by the sucrose gradient method (Palmer, 1986) or as total cellular DNA by a modified CTAB procedure (Doyle & Doyle, 1987) followed by CsCl gradient purification. The *rbc*L gene was isolated for cloning by one of two methods. (1) For most taxa, fragments containing the entire *rbc*L gene were gel-isolated from either Sac I or Sac I/BamHI digests and ligated into the plasmid vector Bluescript (Stratagene, Inc., LaJolla, California). Recombinant, *rbc*L-containing colonies were confirmed by Southern hybridization to cloned *rbc*L fragments from peas. The coding region was sequenced from a single-stranded template by the dideoxy chain termination method (Sanger et al., 1977) using a series of primers based on *rbc*L sequences from maize and spinach (obtained from G. Zurawski, DNAX). (2) Sequences from *Pentas* and *Boopis* were obtained following amplification and cloning of a double-stranded fragment using the polymerase chain reaction following the methods of Olmstead et al. (1992).

Preliminary analyses included 14 new sequences (see Table 1 and Appendix to this issue) and one previously published sequence from *Flaveria* in the Asteraceae (Hudson et al., 1990) and, to serve as outgroups, sequences from *Spinacia* in the Caryophyllidae (Zurawski et al., 1981) and *Nicotiana* in the Asteridae (Shinozaki et al., 1988). These analyses (Michaels & Palmer, 1990) on only a subset of the data reported here identified a closest sister group identical to the present expanded analysis. The results of concurrent studies of *rbc*L sequences in the Saxifragaceae (Soltis et al., 1990), Asteridae (Olmstead et al., 1992), and 499 angiosperms (see Chase et al., 1993) have motivated the inclusion of data from other outgroups and from taxa not previously suspected to be associated with the Asteraceae. Data for *Heuchera* (Soltis et al., 1990), *Magnolia* (Golenberg et al., 1990), *Villarsia*, *Menyanthes*, *Hedera*, and *Coriandrum* (Olmstead et al., 1992) were obtained from published reports, whereas an unpublished sequence for *Corokia* was made available by D. Morgan and D. Soltis.

Although the coding regions for these taxa ranged from 1428 to 1458 bp, only a 1428 bp region was analyzed because no major insertions or deletions were found in this region, allowing alignment by eye, and because homology of positions beyond 1428 is uncertain. Analyses over longer sequences did, however, produce virtually the same results.

TABLE 1. Species of Asteraceae, related families, and outgroups compared by *rbc*L sequence. * = New sequence obtained for this study.

| | |
|---|---|
| Asteraceae | |
| Barnadesioideae | *Barnadesia caryophylla* (Vell.) S. F. Blake* |
| | *Dasyphyllum dicanthoides* (Less.) Cabrera* |
| Chicorioideae | *Lactuca sativa* L.* |
| | *Carthamnus tinctorius* L.* |
| Asterioideae | *Flaveria trinervia* Mohr |
| | *Helianthus annuus* L.* |
| | *Senecio mikanioides* Otto* |
| Related families | |
| Caprifoliaceae | *Viburnum acerifolia* L.* |
| Dipsacaceae | *Dipsacus sativus* Honck.* |
| Valerianaceae | *Valeriana officinalis* L.* |
| Rubiaceae | *Pentas lanceolata* K. Schum.* |
| Goodeniaceae | *Scaevola frutescens* Krause* |
| Campanulaceae | *Campanula ramosa* Sibth. & Smith* |
| Lobeliaceae | *Lobelia erinus* L.* |
| Calyceraceae | *Boopis anthemoides* Jussieu* |
| Apiaceae | *Hedera helix* L. |
| Araliaceae | *Coriandrum sativum* L. |
| Menyanthaceae | *Menyanthes trifoliata* L. |
| Menyanthaceae | *Villarsia calthifolia* F. Muell. |
| Cornaceae | *Corokia macrocarpa* T. Kirk |
| Outgroup families | |
| Chenopodiaceae | *Spinacia oleracea* L. |
| Saxifragaceae | *Heuchera micrantha* Douglas ex Lindl. |
| Solanaceae | *Nicotiana tabacum* L. |
| Magnoliaceae | *Magnolia macrophylla* Michx. |

Analyses were also conducted in which transitions and transversions were differentially weighted (1.0: 1.3, Albert et al., 1993). Since weighted analyses did not alter the tree topologies, only the results of the equally weighted analyses are reported here. PAUP, Phylogenetic Analysis Using Parsimony, Version 3.0r (Swofford, 1991), was used to conduct Fitch parsimony analyses (Fitch, 1971). The HEURISTIC search option with 10 random replicates (Maddison, 1991) was used for tree building and branch swapping under the MULPARS and TBR options. Strict consensus trees were computed. To assess robustness of clades identified in the analyses, the bootstrap method (based on 500 replicates; Felsenstein, 1985) was used. In addition, a "decay" analysis was conducted (cf. Bremer, 1988; Donoghue et al., 1992; Hillis & Dixon, 1989) in which strict consensus trees were generated from all trees five steps longer than the most parsimonious ones. The FILTER TREES option was then used to identify all trees at each shorter tree length. Support for each clade was assessed by determining when each clade was no longer resolved in consensus trees from progressively less parsimonious solutions.

## RESULTS

Of the 1,428 nucleotide positions compared among the 24 *rbc*L sequences in the analysis, 452 were variable. Exclusion of autapomorphies resulted in 278 potentially synapomorphous characters, 204 of which were at third-codon positions, 45 at first, and 29 at second. The third position characters are essential sources of phylogenetic information, as their elimination from the data set results in little resolution (data not shown). Initial analyses (results not shown) used four taxa [*Magnolia* (Magnoliidae), *Spinacia* (Caryophyllidae), *Heuchera* (Rosidae), and *Nicotiana* (Asteridae)] as designated outgroups. These analyses established *Nicotiana* as the sister group to an ingroup consisting of the taxa proposed as outliers to Asteraceae. In subsequent analyses, the more distant outgroups *Magnolia*, *Spinacia*, and *Heuchera* were deleted, and trees were arranged using *Nicotiana*

alone as the designated outgroup. The heuristic search found four equally parsimonious trees (results not shown) of 833 steps with consistency index (C.I.) of 0.48 (autapomorphies excluded) and a retention index (R.I.) of 0.502. The strict consensus of the four trees (Fig. 1) shows a large, nested monophyletic group consisting of the Asteraceae, Goodeniaceae, Calyceraceae, *Corokia* (Cornaceae sensu Cronquist, 1981), Menyanthaceae, Lobeliaceae, and Campanulaceae. The two polytomies exist in either a more basal portion of the tree or within the Asteraceae. Among the putative relatives of the Asteraceae examined here, *Pentas* (Rubiaceae) was placed as the most basal clade. As in our earliest analysis with only a subset of these data, the expanded analysis identifies a clade consisting of *Scaevola* (Goodeniaceae) and *Boopis* (Calyceraceae) in the most proximal position to the Asteraceae. This sister relationship is supported by eight shared nucleotide substitutions.

The robustness of the sister relationship of the Goodeniaceae–Calyceraceae clade to the Asteraceae is indicated by two subsequent analyses. First, the results from 500 bootstrap replications using the heuristic search option indicate that this relationship is one of the more robust areas of the tree topology, occurring in 84% of the trees (Fig. 2). Relationships are, with some exceptions, poorly resolved within the Asteraceae (also see Kim et al., 1992) and also outside the "Asterales" (Lobeliaceae–Campanulaceae through Asteraceae) clade. Within the "Asterales" are three other well-supported groups besides the Asteraceae–Goodeniaceae–Calyceraceae clade: (1) the Asteraceae emerge as monophyletic in 97% of the bootstrap trees, (2) Campanulaceae and Lobeliaceae occur together in all bootstrap replicates, (3) the Goodeniaceae and Calyceraceae clade is monophyletic 86% of the time. Finally, the "Asterales" group as a whole appears in 86% of the trees.

Second, the strength of the relationship of the Goodeniaceae–Calyceraceae clade to the Asteraceae is indicated in the decay analysis by the persistence of this group in less parsimonious solutions. The sister position of this clade is maintained in 127 trees up to two steps longer than the most parsimonious trees. The strict consensus tree at three additional steps places the Goodeniaceae–Calyceraceae clade within an unresolved polytomy together with various unresolved lineages of the Asteraceae, while the Asteraceae–Goodeniaceae–Calyceraceae group forms an unresolved polytomy with the rest of the "Asterales" (*Villarsia*, *Corokia*, *Menyanthes*, *Campanula–Lobelia*). When the 964 trees up to four steps longer are included, most of the resolution in the tree is lost, and all but the strongest clades (i.e., Goodeniaceae–Calyceraceae, Campanulaceae–Lobeliaceae, Valerianaceae–Dipsacaceae, and *Helianthus–Flaveria*) disintegrate.

## Discussion

The *rbc*L data clearly indicate a close relationship among the Asteraceae and other families traditionally placed in the Asterales and Campanulales. This conclusion is supported not only in the local analysis presented here, but also in much broader analyses of the Asteridae (Olmstead et al., 1992, 1993) and in an analysis of 499 *rbc*L sequences from seed plants (Chase et al., 1993). The placement of the Campanulaceae, Lobeliaceae, Goodeniaceae, Calyceraceae, and Asteraceae in a single monophyletic group is consistent with the system of relationships proposed by Takhtajan (1987) and Thorne (1992), in which these groups (together with families in the Stylidiales) form the superorder Asteranae. This grouping is also distinguished in the system of Wagenitz (1977) and the recent review by Lammers (1992), but not in the systems proposed by Dahlgren (1975) or Cronquist (1981). Dahlgren aligned the Goodeniaceae and the Calyceraceae far from the Asteraceae, placing them in the Gentiananae and Cornanae, respectively. The topology inferred from the *rbc*L data is most divergent from the Cronquist system. Although Cronquist placed the Goodeniaceae together with the Campanulaceae and other families to form Campanulales, the Calyceraceae were assigned to the Dipsacalean group, while the Asteraceae were placed nearest the Rubiaceae. The latter association is clearly not supported by the *rbc*L data; *Pentas* (Rubiaceae) was consistently placed in the most distant position of all the putatively allied families under consideration as sister groups in this analysis.

The sister-group relationship of the Goodeniaceae–Calyceraceae clade to the Asteraceae is supported by evidence from a number of studies. The pollen-presentation mechanisms of the Goodeniaceae, Calyceraceae, and Asteraceae are similar, and they also resemble the mechanisms of the Campanulaceae, Lobeliaceae, and Brunoniaceae (Erbar & Leins, 1989; Leins & Erbar, 1990; Lammers, 1992; Wagenitz, 1992). Details of floral development (Harris, 1991; Erbar & Leins, 1989) also unite both Goodeniaceae and Calyceraceae with the Asteraceae. However, the particular development pattern they share is also found in Brunoniaceae, Campanulaceae, Stylidiaceae, Menyan-

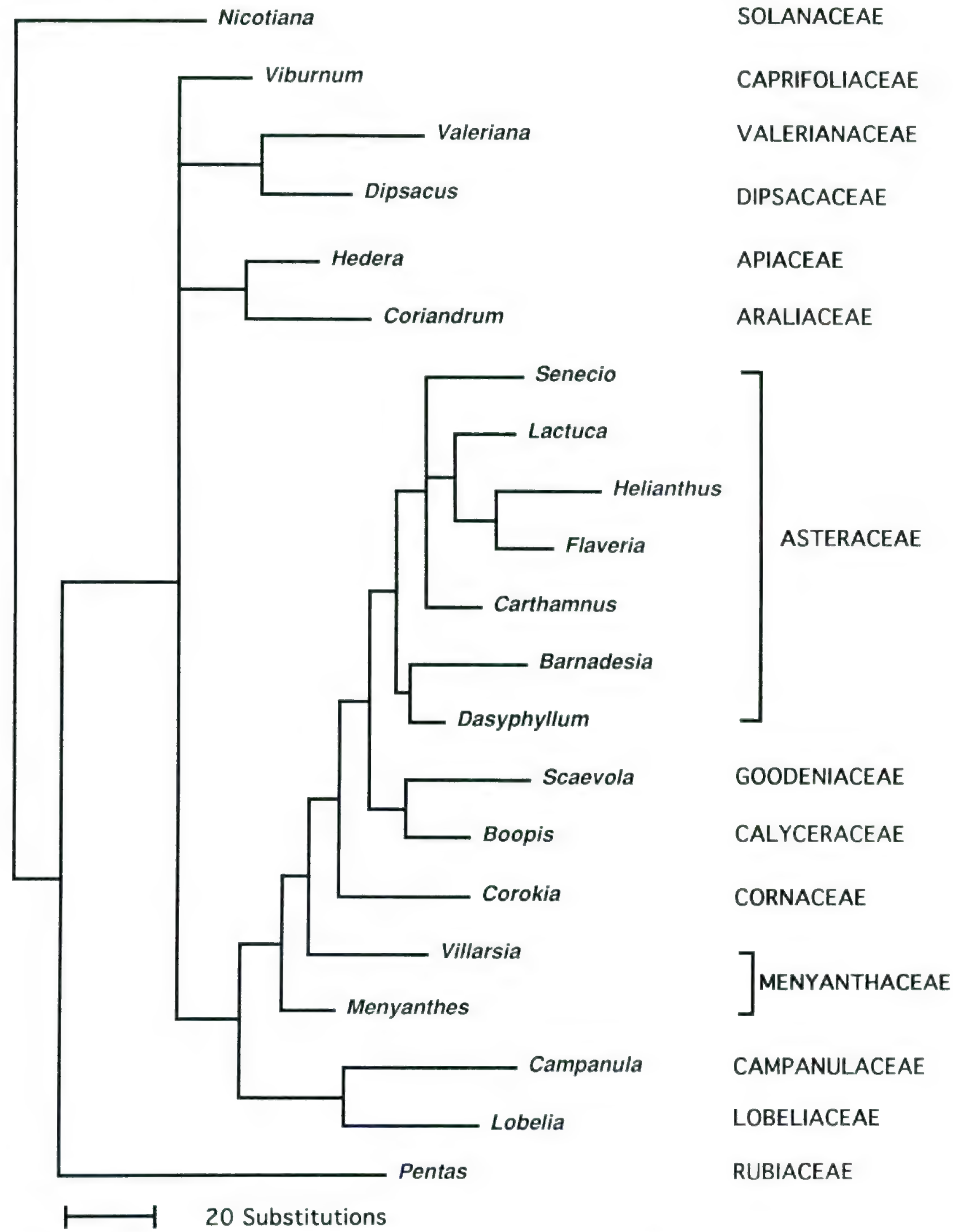


FIGURE 1. Strict consensus of four equally parsimonious trees (length = 833 steps, C.I. = 0.48, R.I. = 0.50) based upon *rbc*L sequences. Branch lengths are proportional to the number of nucleotide substitutions supporting a node or distinguishing a terminal lineage (note scale at bottom).

thaceae, Rubiaceae, and families of the Dipsacales (Erbar & Leins, 1989), and therefore this is probably a plesiomorphic character. Chemical characters such as carbohydrate storage as inulin (in Asteraceae, Calyceraceae, and Goodeniaceae, as well as Menyanthaceae, Campanulaceae, and Lobeliaceae; Pollard & Amuti, 1981) and phenolics (e.g., caffeic acid in Asteraceae, Calyceraceae, and

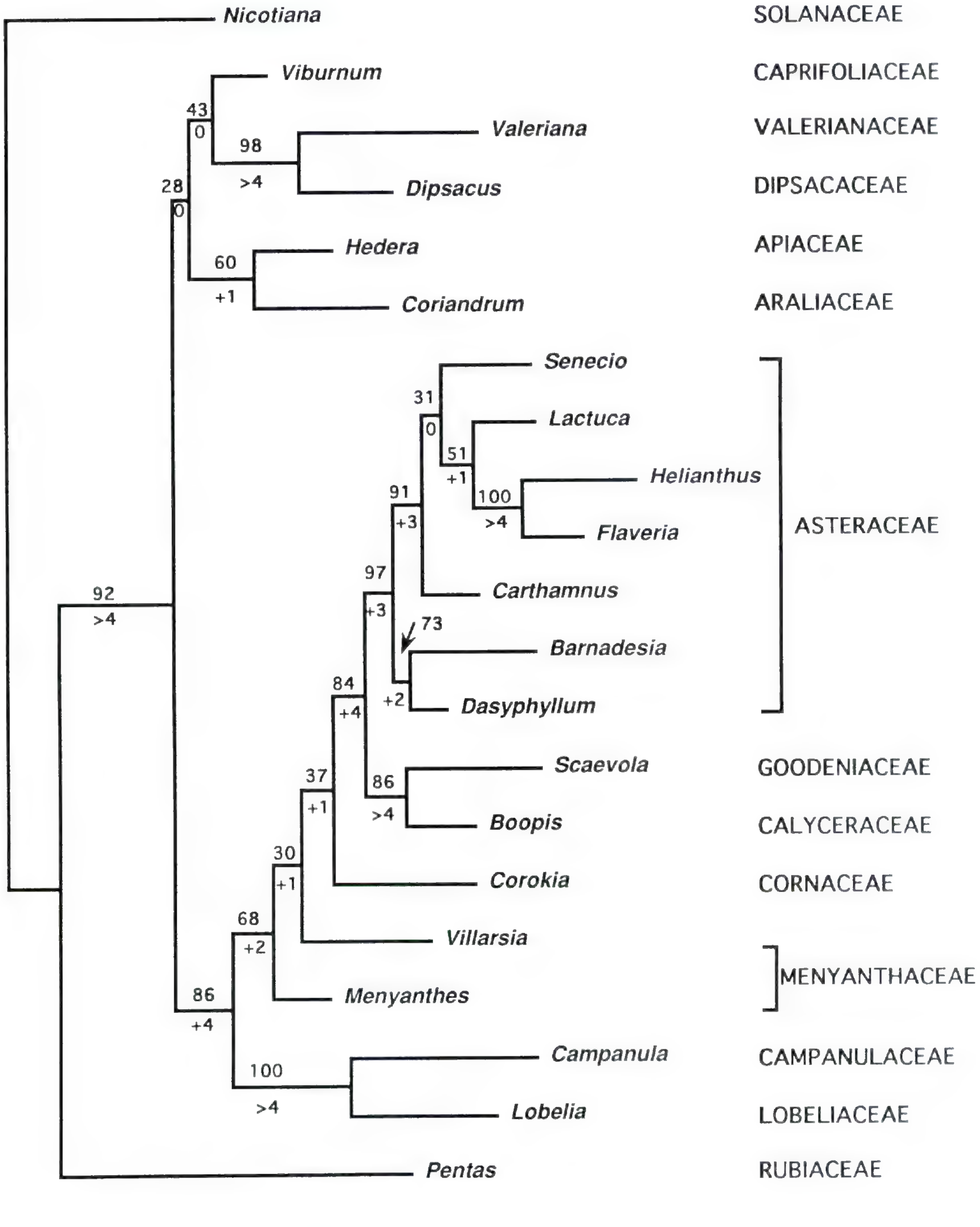


FIGURE 2. One of the four equally parsimonious trees based upon *rbc*L sequences with the results of the bootstrap and decay analyses. Branch lengths are proportional to the number of nucleotide substitutions supporting a node or distinguishing a terminal lineage (note scale at bottom). Bootstrap values from 500 replications are indicated above the branches. Numbers below indicate numbers of additional steps needed for a branch to collapse.

Goodeniaceae, as well as Menyanthaceae and Campanulaceae; Lammers, 1992) further support the position of the Goodeniaceae and Calyceraceae. Asteraceae, Goodeniaceae, and Calyceraceae also lack endosperm haustoria, have binucleate tapetal cells, and produce herbivore defenses through the mevalonate pathway, characters that are also shared with Menyanthaceae, but are absent from Campanulaceae and Lobeliaceae (Lammers, 1992).

Several other characters specifically support the sister placements of Goodeniaceae or Calyceraceae alone. Polyacetylenes, which are characteristically found in the Asteraceae, have also been reported from some Campanulaceae (Ferreira & Gottlieb, 1982), Lobeliaceae, and one Goodeniaceae (Lammers, 1992). Their distribution in Calyceraceae, Menyanthaceae, or other families that place near the Asteraceae in our analysis is unknown. The Calyceraceae were proposed as a sister group to the Asteraceae by Jeffrey (1977). Evidence in support of the placement of Calyceraceae seen in our *rbc*L analyses derives from chloroplast DNA restriction site data (Downie & Palmer, 1992a; unfortunately, due to their unusual genome organization, Goodeniaceae could not be included in this study) and floral development, as noted above, but also from pollen morphology, capitulum structure, and biogeography. Skvarla et al. (1977) concluded that the ultrastructure of Calyceraceae exine is nearly identical to that of the Asteraceae, while the Goodeniaceae are among five families listed with pollen similar enough to "suggest distinct linkages." As previously advocated by Turner (1977), the structurally homologous capitula and floral features, and congruent core distributions of the Asteraceae and Calyceraceae in South America are particularly compelling arguments supporting a shared phylogenetic history.

This analysis suggests a particularly strong sister-group relationship for the Goodeniaceae and Calyceraceae, occurring in 86% of the bootstrap trees. This clade also remained intact throughout the decay analysis, a level of association seen only in other groups that have traditionally been strongly linked (e.g., *Helianthus* and *Flaveria* in the Heliantheae; Campanulaceae and Lobeliaceae; Dipsacaceae and Valerianaceae). As noted above, the Goodeniaceae and Calyceraceae are united by several characters, including pollen-presentation mechanism, floral development, pollen embryology, and secondary chemistry (e.g., seco-iridoids; Lammers, 1992). The *rbc*L trees and above evidence supporting the placement of the Goodeniaceae (a small family of 325 species distributed primarily in Australia and Tasmania) and the South American Calyceraceae are consistent with Turner's (1977) proposal of a Gondwanaland origin for the Asteraceae. Indeed, all the closest groups from Menyanthaceae to Goodeniaceae are distributed primarily in the Southern Hemisphere.

The *rbc*L gene was recently sequenced from two families previously suggested to have affinities with the Asteraceae (Olmstead et al., 1992). Both the Apiaceae (*Hedera*) and Araliaceae (*Coriandrum*) have been proposed as close associates of the Asteraceae based upon shared phytochemistry (Hegnauer, 1964, 1977). However, Lammers (1992) has argued that the synthesis of sesquiterpene lactones in these groups is due to parallel evolution. Parsimony analyses of *rbc*L indicate that, although neither is closely related to the Asteraceae, these groups do belong in the Asteridae rather than in their more traditional position in the Rosidae (Olmstead et al., 1992, 1993; Chase et al., 1993).

Although neither Menyanthaceae nor Cornaceae have ever been allied with the Asteraceae based on traditional data, they were included in this study because other recent chloroplast DNA analyses suggested close relationships. Based on *rbc*L sequences, Olmstead et al. (1992) found an unexpected association of the Menyanthaceae with the families more typically suggested to have affinities with the Asteraceae. A survey of restriction sites in the chloroplast DNA inverted repeat (Downie & Palmer, 1992a) also places the Menyanthaceae along with the Calyceraceae and Asteraceae. The most parsimonious solutions from Olmstead et al. (1992, 1993), which are based on a much larger sampling of taxa within the Asteridae, are consistent with the results reported here. Although Menyanthaceae are nearer to the Asteraceae than either the Campanulaceae or Lobeliaceae in this study, Calyceraceae retain the sister position (Goodeniaceae were not included in the Asteridae analyses of either Olmstead et al., 1992, or Downie & Palmer, 1992a). Several features shared by Menyanthaceae, Calyceraceae, and Goodeniaceae (the production of seco-loganin, carbohydrate storage as inulin, presence of multinucleate tapetal cells, absence of endosperm haustoria, and chromosome numbers based upon $x = 8$ or 9; Lammers, 1992) are consistent with the placement of Menyanthaceae in these analyses.

In addition, the analyses of Morgan & Soltis (1993) and Chase et al. (1993) indicate an unsuspected affiliation of *Corokia* (Cornaceae sensu lato) with the asteralean clade. The association of *Corokia* with Asteraceae and its near relatives was

confirmed in our analyses, which are more likely to produce optimal solutions, while the computational difficulties of the much larger analyses (Chase et al., 1993; Morgan & Soltis, 1993) may have precluded discovery of shortest trees. This radical departure from previous placements of *Corokia* (in Escallonioideae, Saxifragaceae sensu lato, Engler, 1928; in Cornaceae, Eyde, 1966 and Cronquist, 1988; or in Araliaceae, Phillipson, 1967) is consistent with several other characters: (1) biogeography (*Corokia* is distributed primarily in New Zealand and Australia; Eyde, 1966), (2) some aspects of morphology (inferior ovary, locules 1–3 with a single, apical, unitegmic ovule, and multicellular, T-shaped trichomes, found elsewhere only in the Asteraceae and three other unrelated families; Eyde, 1966), and (3) chemistry (presence of iridoids in Escallonioideae; Dahlgren et al., 1981). See also Morgan & Soltis (1993) for further discussion of evidence linking genera of the Escallonioideae with Asteridae. These unanticipated associations not only illustrate the heuristic value of the broader analyses and the benefits of widespread data sharing, but also motivate the acquisition of additional data from other sources that may corroborate these new hypotheses of relationships. For example, studies of floral developmental patterns, pollen ultrastructure and development, and embryogeny in Menyanthaceae and *Corokia* would be a logical direction for future work.

Finally, although many families that have been previously considered as serious contenders for sister group to the Asteraceae have been investigated in this study, several others remain to be examined. In particular, Brunoniaceae and Stylidiaceae have been associated with Asteraceae and Campanulaceae in Takhtajan's (1987), Wagenitz's (1977), and Thorne's (1992) classifications. Both are distributed primarily in Australia and share the floral developmental features found in Asteraceae, Campanulaceae sensu lato, Goodeniaceae, and Calyceraceae (Erbar, 1991). Brunoniaceae also possess a similar pollen-presentation mechanism to those found in the first three of these families (Leins & Erbar, 1990). Any comprehensive attempt to further explore the origins of the Asteraceae should include several other, poorly understood small families that have also been associated with Campanulales (Pentaphragmataceae, Cyphiaceae, and Sphenocleaceae; Lammers, 1992). The addition of data from these groups is likely to provide new insights into the phylogeny of the Asteraceae and further resolve the current picture of relationships of this distinctive lineage.

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# CHARACTER-STATE WEIGHTING FOR CLADISTIC ANALYSIS OF PROTEIN-CODING DNA SEQUENCES[1]

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## ABSTRACT

Nucleotide data are a restricted character system complex enough to confound phylogenetic analyses yet simple enough to permit establishment of probability models for sequence change and corresponding character-state weighting schemes. We have previously developed a general method for weighting DNA data that is here elaborated for protein-coding sequences. Included in the present model are corrections for (i) multiple substitution events, (ii) transition/transversion bias, and (iii) differential proportions of changes occurring at first, second, and third codon positions. This model is shown to be generally consistent for all phylogenetically useful data. Greater understanding of the properties of equal versus differential character-state weighting comes from consideration of numbers of terminal taxa and lengths of tree segments. With insufficient sampling of taxa, differential weighting attempts to correct for undetected multiple substitution events. Both equal and differential weighting should give the same result if sufficient numbers of terminal taxa permit the detection of historically misleading character-state changes. Nevertheless, spurious attraction of tree segments remains a systematic problem that is not easily resolved either by equal weighting or by our differential weighting model, which acts globally rather than adjusting for different probabilities of character-state change among tree segments. Artifactual segment attraction is best understood in terms of asymmetries in $\lambda$ (which represents state changes per character during a particular segment interval). We relate the consistency index to numbers of terminal taxa and $\lambda$, illustrating its dependence upon numbers of potential tree segments. Prospects for phylogenetic reconstruction from protein-coding nucleotide data are discussed with reference to the robustness of equal weighting (given our own model) with adequate taxonomic sampling.

Information derived from nucleotide sequences is becoming increasingly popular for phylogenetic studies, partially because of technological advances (such as automatic temperature cyclers and thermostable polymerases) that permit rapid and extensive data gathering. The deceptively simple properties of DNA data and their promise of more reliable phylogenetic hypotheses have changed the research emphasis of many systematists. DNA variation can indeed provide valuable characters for phylogenetic reconstruction when treated with an appropriate understanding of its properties, but it is not a panacea for phylogenetics (contra Gould, 1985). Reflecting perhaps a lack of understanding of first principles, too many cladograms derived from both molecular and morphological data are appearing in the literature without justified character analysis or choice of optimality criterion. Although our current understanding of molecular biology may be superior to that of the ontogeny and heritability of most morphological characters, "simple" molecular phenomena such as multiple substitution at particular sites (e.g., Brown et al., 1982) and paralogy in multigene families (Fitch, 1970) can confound phylogenetic analysis.

The apparent simplicity of DNA data in comparison with other data forms can be misleading. The pattern of DNA variation *is* simpler compared to most morphological data in that there are four basic character states (the nucleotides A, C, G, and T) with no intrinsic ordering into a transformation series. However, evolutionary independence of nu-

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cleotide positions (a requisite if they are to be used as characters in cladistic analysis) cannot be automatically assumed. Protein-coding sequences are organized into triplet nucleotide codons that may be positionally intra- and interdependent because of constraints imposed by the genetic code and the function of the encoded protein. Such constraints may produce unequal and correlated probabilities of substitution among nucleotide positions (see Fitch & Markowitz, 1970; Fitch, 1986). Positional homology of nucleotides may be relatively easy to determine, but hypotheses of *character-state* homologies can be confused by multiple, undetected substitutions, which are themselves drawn from the same four possible states. Despite these underlying complexities, it has been possible to derive simple probability models that mimic properties of sequence evolution (e.g., Albert & Mishler, 1992; Albert et al., 1992; DeBry & Slade, 1985; Felsenstein, 1981a, 1992; Hendy, 1989; Hendy & Penny, 1989; Lanyon, 1988; Templeton, 1983). Some of these models have, in turn, been applied to maximum-parsimony inference of cladistic relationships (e.g., Albert et al., 1992; Chase & Palmer, 1992; Donoghue et al., 1992; Gastony et al., 1992; Kadereit & Sytsma, 1992; Olmstead & Palmer, 1992; Spooner & Sytsma, 1992; Wendel & Albert, 1992).

Characters and character states for cladistic analysis of DNA sequences are derived from either indirect or direct sequence sampling. The most widely used indirect approach is mapping of restriction endonuclease cleavage sites. When a particular restriction site is found to be present in some terminal taxa and absent in others, an underlying sequence difference is implied de facto. Wagner parsimony (Farris, 1970; Kluge & Farris, 1969) places no restrictions on underlying patterns of nucleotide substitution. In contrast, the Dollo criterion (Farris, 1977; see also Farris, 1983: 24–26) will not recognize substitutions that could lead to parallel gain of a recognition sequence, although parallel losses are tolerated. In a previous paper, we developed a character-state weighting scheme that treats both forms of homoplasy relative to differential probabilities of gain versus loss estimated for individual restriction sites (Albert et al., 1992).

The reasoning developed by Albert et al. (1992) was extended to direct sequence sampling by Albert & Mishler (1992); a character-state weighting scheme was erected to recognize the asymmetrical probabilities of transversion versus transition substitutions within nucleotide characters. Here, the model of Albert & Mishler (1992) is modified to incorporate asymmetrical probabilities of substitution among codon positions in protein-coding sequences. The model rests on the simplifying assumption of equal probability of change among first, second, and third codon positions (respectively). The model also provides a correction for multiple substitutions at particular positions and accommodates wide ranges of branch lengths, transition/transversion ratios, and codon position biases. After explaining the assumptions underlying our approach, we provide a heuristic examination of its properties by comparing it with the commonly used, equal-weighting parsimony criterion of Fitch (1971, 1977: a nonadditive, multistate generalization of the Wagner criterion; Farris, 1970; Kluge & Farris, 1969; cf. Swofford & Olsen, 1990). We evaluate consistency criteria in terms of permissible branch-length asymmetries and discuss expectations based on the number of taxa analyzed; branch length is incorporated into the consistency index (Kluge & Farris, 1969) to explain its dependence upon taxon number. We conclude with prospects for phylogenetic analysis of protein-coding sequence data, including the recognition that equal weighting is a robust assumption given a relatively even sampling of the true tree.

## The Model

Our previous character-state weighting models for restriction site (Albert et al., 1992) and nucleotide sequence data (Albert & Mishler, 1992) were designed for utility of execution. We have opted for simplified representations of the major known biasing factors in molecular evolution to provide generalized, robust weighting schemes employable with large numbers of taxa. Within-character weighting is easily accomplished by representing transformational costs between states in matrix form (Fitch & Ye, 1991; Sankoff & Cedergren, 1983; Swofford & Olsen, 1990; Williams & Fitch, 1989, 1990). As of this writing, stepmatrix weighting is available in PAUP 3.0 (Swofford, 1991), MacClade 3.0 (Maddison & Maddison, 1993), and a program available from Walter M. Fitch (Williams & Fitch, 1990). Application of stepmatrices is computationally expensive relative to Fitch parsimony because it requires dynamic programming (Sankoff & Cedergren, 1983; Swofford & Olsen, 1990). With PAUP 3.0, a single stepmatrix may be assigned to an entire data set, or individual stepmatrices may represent each character separately. If one understood how each nucleotide position bears on protein function, one could possibly assign individual probability models and individual weight-

ing stepmatrices over an entire sequence. This is not currently practical because it would require comparison across many taxa that in turn would have to be associated with a robust phylogenetic hypothesis. Furthermore, as will be shown below, minor heterogeneities in transformational probabilities have negligible effects on parsimony reconstructions.

## BRANCH LENGTH AND THE UNITS OF CHARACTER-STATE CHANGE

Branch length, $\Lambda$, refers to the total number of changes expected along a tree segment connecting either two nodes or a node to a terminal. In some models, including ours (Albert & Mishler, 1992; Albert et al., 1992; DeBry & Slade 1985), $\lambda$ is the symbol used to express branch length in per-character terms, i.e., $\Lambda = \Sigma \lambda_i$ over $I$ characters (where $\Sigma i = I$). This usage should not be confused with $\lambda$ = rate of character-state change with respect to time (a usage employed, for example, by Hendy, 1989; Hendy & Penny, 1989; Nei, 1987). That rate was referred to as $S_r$ by Albert et al. (1992), i.e., the *effective* substitution rate for a character (a nucleotide string of any defined length); effective substitutions are those that have been fixed in a lineage. The expected number of changes per character during a segment, $\lambda$, is thus equal to the product of the rate of change, $S_r$, and the time through which the branch existed, $T$. The units of time cancel, yielding a parameter that is expressed in terms of state changes per character per segment. Therefore, different combinations of rates and times can yield the same $\lambda$ value.

Observed mean branch length over all characters and all segments ($\bar{\lambda}$) can be used to estimate $\lambda$ under the simplifying assumption that all segments are of equal length (see discussion below on effects of unequal segment lengths). Because the number of segments in an unrooted tree is $[2n - 3 - p]$, where $n$ = the number of taxa, and $p$ = the number of segments in excess of 3 per node (i.e., polytomies),

$$\bar{\lambda} = \Delta/([2n - 3 - p]I) \qquad (1)$$

where $\Delta$ is the number of character-state changes observed over an entire tree and $I$ is the number of characters represented. An average $\lambda$ may also be estimated for the $i$th character over all segments:

$$\bar{\lambda}_i = \Delta_i/[2n - 3 - p] \qquad (2)$$

Likewise, branch lengths may represent averages for a specific set, $A$, of all characters $I$:

$$\bar{\lambda}_{I_A} = \Delta_{I_A}/([2n - 3 - p]I_A) \qquad (3)$$

Expression (1) was the strategy used by Albert et al. (1992) and recommended by Albert & Mishler (1992) for estimating $\bar{\lambda}$ values from DNA sequence data optimized onto robust, a priori cladistic hypotheses based on other character systems (see below). For the present purpose, however, individual $\bar{\lambda}_{I_i}$ values for each codon position are required. The simplest way to produce such values is to partition $\bar{\lambda}$ estimates with three multipliers ($\alpha_1$, $\alpha_2$, $\alpha_3$) representing the fraction of substitutions per codon position observed on an a priori topology.

## PROBABILITIES OF CHARACTER-STATE TRANSFORMATIONS

The premise behind the nucleotide character-state weighting model described by Albert and Mishler (1992) is that the probability of observing a transition is different (greater, in most cases) from that of observing a transversion. This asymmetry can be estimated by phylogenetic comparisons of sequences; nucleotide state changes are optimized onto an a priori cladogram, which provides a "phylogenetic correction" for multiple substitutions (Albert and Mishler, 1992; Albert et al., 1992). The phylogenetic correction does not reflect *all* substitutions that have occurred, only those that are effectively fixed in lineages and are observable given the taxa sampled (as will be discussed in detail below, if too few taxa are sampled, many multiple substitutions will go undetected). The Kimura two-parameter model (K2P; Kimura, 1980), which was designed to take into account transition and transversion information in order to estimate net substitutions in pairwise comparisons, provides a similar, albeit slightly higher, estimation of substitutions than does the phylogenetic estimate mentioned above (Albert et al., 1992). The K2P model has been reoriented for estimating transformational probability on phylogenetic trees by Swofford & Olsen (1990; in terms of transition and transversion rates) and by J. Felsenstein (cited in Albert & Mishler, 1992). Felsenstein's formulations are more useful for the present purpose because there are only two parameters—$\lambda$ and transition/transversion ratio (R):

$$P_{xi}(T) = \tfrac{1}{4} + \tfrac{1}{4}\exp\left[-\lambda\frac{1}{(\tfrac{1}{2})(1 + R)}\right] - \tfrac{1}{2}\exp\left[-\lambda\frac{(\tfrac{1}{2}) + R}{(\tfrac{1}{2})(1 + R)}\right] \qquad (4)$$

where $xi$ indicates that the probability is for a particular *transition*, and

$$P_{xv}(T) = \tfrac{1}{4} - \tfrac{1}{4}\exp\left[-\lambda\frac{1}{(\tfrac{1}{2})(1 + R)}\right]; \quad (5)$$

where $xv$ indicates that the probability is for a particular *transversion*.

Determining differential transformational probabilities for each of the three codon positions requires partitioning $\bar{\lambda}$ with the $\alpha_1$, $\alpha_2$, and $\alpha_3$ multipliers. As a result, three separate calculations for both expressions (4) and (5) are required. The partitioned $\bar{\lambda}\alpha$ values used here assume equal probabilities of character-state change within all first, second, and third codon positions, respectively. These probabilities only consider change as a function of entire trees (through the use of $\bar{\lambda}$); no adjustment is made for individual segments. These assumptions, although defensible as a first approximation, are simplifications relative to the covarion and covariotide hypotheses (Fitch & Markowitz, 1970; Fitch, 1986; cf. Hendy & Penny, 1989; Fitch & Ye, 1991) and branch-length asymmetries that may be present on true trees.

## CHARACTER-STATE WEIGHTS

Transformational probabilities and their corresponding character-state weights share a simple mathematical relationship. In fact, the following historical discussion highlights a conceptual link between maximum parsimony and maximum likelihood approaches to phylogenetic inference. In his Bayesian approaches to cladistic analysis, Farris (1973, 1977, 1978, cf. 1983, 1986) examined the posterior probability of a phylogenetic hypothesis—$P(hypothesis|data)$—through its proportionality to the joint probability—$P(hypothesis, data)$—for a given data matrix. This follows from Bayes's (1763) theorem of conditional probability:

$$P(hypothesis|data) = [P(data|hypothesis)P(hypothesis)]/P(data) \quad (6)$$

From expression (6), the following simplification can be made:

$$P(hypothesis|data) = [P(hypothesis,data)]/P(data) \quad (7)$$

For a particular parsimony analysis, the prior probability of the data, $P(data)$, is constant and the prior probability of a particular maximum parsimony tree, $P(hypothesis)$, may be considered equal over all such trees. Farris's derivation of $P(hypothesis,data)$ was expressed as repeated products of state transformation probabilities and their assignments to tree segments over all characters. Thus, $-\ln[P(hypothesis,data)]$ took the form of summation of these statements; by the nature of logarithms, minimizing the latter expression (and so tree length) is equivalent to maximizing the former (i.e., finding the tree length of greatest probability). Log-transformed probability factors not solely dependent upon the data matrix were considered to represent weights for character-state changes. Summation of these weights over all characters and their segment assignments (i.e., to produce a weighted tree-length) was interpreted as identical to the weighted parsimony criterion of Kluge & Farris (1969). Thus, taking the natural logarithm of $P(hypothesis,data)$ permits calculation of both character-state weights and the minimum number of weighted steps required to produce the most probable (i.e., most parsimonious) tree.

A similar argument for logarithmic conversion of probabilities into weights comes from maximum likelihood inference (Felsenstein, 1981b; cf. critique by Farris, 1983). From Bayes's theorem (Bayes, 1763; expression 6), likelihood—$P(data|hypothesis)$—is also proportional to the joint probability $P(hypothesis,data)$, but through $P(hypothesis)$ rather than $P(data)$:

$$P(data|hypothesis) = [P(hypothesis,data)]/P(hypothesis) \quad (8)$$

Likelihood depends entirely upon the model constructed for $P(hypothesis)$, as evident from different interpretations of the relationship between likelihood and parsimony obtained under different models (Farris, 1973; Felsenstein, 1973; cf. Sober, 1988). Felsenstein's likelihood justification of parsimony (1981b; see also Sober, 1988) involved a simple probability model in which binary data were assumed to contribute the bulk of the likelihood via a single (versus homoplastic) reconstruction of character states. In finding the maximum of the likelihood (nested repeated products), it is customary to find the natural logarithm of the expression (to produce nested summations and simpler calculation of minima; cf. Swofford & Olsen, 1990). Under Felsenstein's assumption of low rates of change (see discussion below), the log-likelihood term for a change of character $i$ in segment $j$ is simply $\ln(\lambda_{ij})$, based on Felsenstein's notation (1981b, his equations 4 and 5). The logarithm of $\lambda_{ij}$ will be negative when $\lambda_{ij} < 1$ and becomes more so as branch length decreases. Felsenstein (1981b) interpreted $|-\ln(\lambda_{ij})|$ values to represent the weights for such changes. Large weights reflect small probabilities of character-state change and vice versa (precedents for this relationship exist,

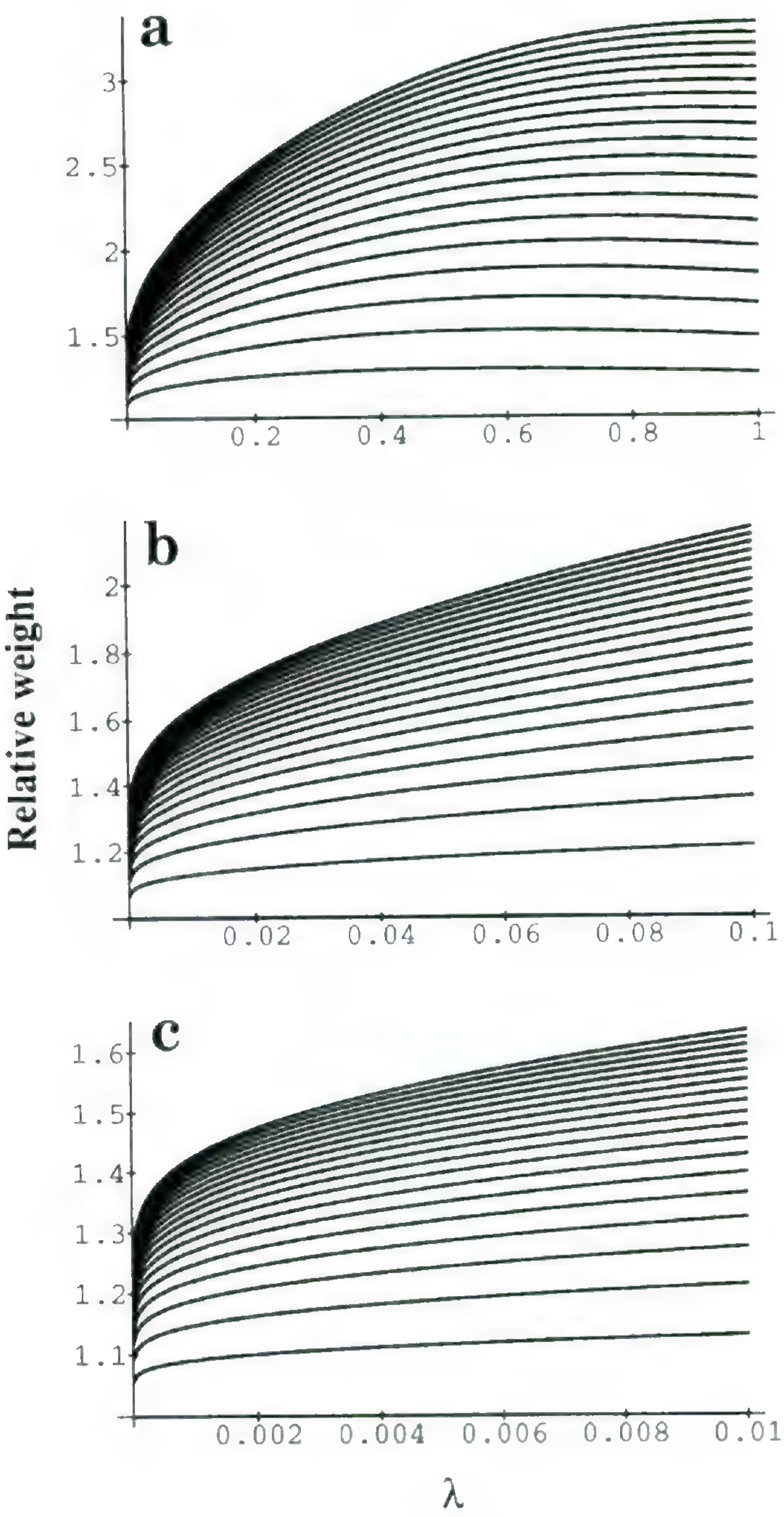


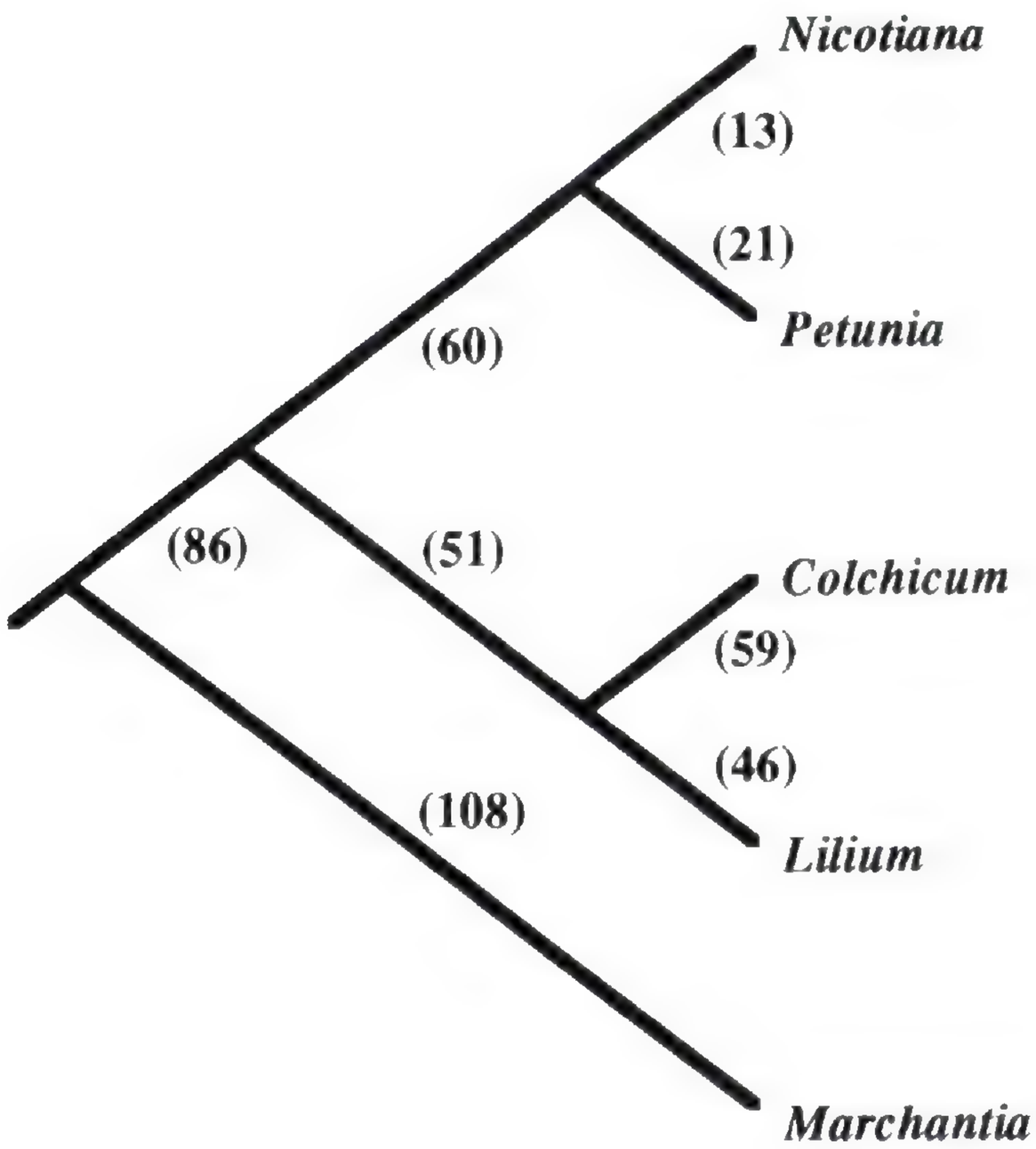

FIGURE 1. Relative weight of nucleotide character-state transformation (transversion weight divided by transition weight; Y axis) as a function of λ (X axis) and differential transition/transversion ratios (represented by the individual curves). λ values between 0 and 1.0 are represented in a; the smaller ranges from 0 to 0.1 and 0 to 0.01 are represented in b and c, respectively. Weights were determined from the ratio of the negative natural logarithms of probabilities obtained from expressions (5) and (4). Transition/transversion ratios evaluated (shown in increasing order along the X axis) were 0.5 (the ratio for randomness from a given starting nucleotide; thus, the result lies directly on the X axis, indicating equal weight) through 10.0 in increments of 0.5.

although suggested on other grounds or under different models; Farris, 1966, 1969, 1977, 1978; Kluge & Farris, 1969). Because likelihood inference chooses the topology that maximizes the likelihood, character-state changes with relatively large weights will be preferentially avoided (Felsenstein, 1981b). Maximizing the logarithm of the likelihood minimizes the sum of the weights of all character-state changes: hence the justification for weighted parsimony, which de facto minimizes the contribution of strongly weighted state transformations.

For the present model, character-state weights for a transversion over a transition are the ratios of the negative natural logarithms of expression (5) probabilities to those of expression (4). The behavior of these weights under a range of values for λ and R can be examined using two-dimensional plots (Albert & Mishler, 1992). In Figure 1, curves representing transition/transversion ratios (R) between 0.5 (parity) and 10 are shown as λ increases continuously from 0 to 1 (the ranges 0 → 0.01, 0 → 0.1, and 0 → 1 are shown separately). As would be expected, the weight approaches 1 as λ becomes smaller. The effect of increasing R is immediately apparent: as transitions become proportionally more frequent, a higher relative weight is assessed to a transversion. Another property of the weighting model is that the relative weight range for transversions over transitions is extremely shallow when λ is small (i.e., < 0.1). Albert et al. (1992) considered λ in some detail from a heuristic mathematical perspective and concluded that λ values ≤ ≈0.1 should be the limit for data that could be expected to reflect phylogenetic history (a λ of 0.1 is equivalent to 1 out of 10 characters changing per tree segment, on average). Under such conditions, $\bar{\lambda}\alpha$ partitions cannot yield substantially different codon position weights using any reasonable value of R (Fig. 1).

## INITIAL WEIGHTS FROM A PRIORI INFORMATION

Because the transversion/transition weight range is so small over all reasonable λ and R values, one could simply use weights (partitioned with appropriate $\bar{\lambda}\alpha$ values) that span this range (i.e., between 1 and ca. 2.2; Fig. 1b) in a series of analyses to search for robust topologies (see Albert et al., 1992). An alternative is to use a priori approximations of $\bar{\lambda}$, transition/transversion ratio, and proportions of substitutions among codon positions to provide initial weighting criteria for a single, optimal phylogenetic reconstruction. Such estimates of $\bar{\lambda}\alpha$ and R values are best derived by optimizing sequence data onto topologies accepted a priori based on robust cladistic analyses of other character systems; attempting to derive estimates solely from the data matrix at hand risks circular reasoning (see Albert & Mishler, 1992; Albert et al., 1992). If such estimates are to be useful, the a priori topology must be encompassing relative to the data to be analyzed, circumscribing variation within it




**total positions = 1398**
**total changes = 444**
**segments = 8**

**transitions = 267**
**transversions = 177**
**1st position changes = 75**
**2nd position changes = 32**
**3rd position changes = 337**

FIGURE 2. "Land plant" tree, modified from Albert et al. (1992). Accepted a priori based on robust cladistic analyses of morphological, anatomical, and biochemical information. Sequence data for *rbc*L (1,398 putatively homologous positions; corrected for 30-bp, 5′-primer nucleotides from the 1,428 positions used by Albert et al., 1992) were constrained to fit this rooted topology using ACCTRAN optimization (Swofford & Maddison, 1987). The numbers in parentheses at each of the 8 tree segments indicate the hypothesized numbers of character-state changes, totalling 444 for the entire tree. Thus, $\bar{\lambda}$ = 444/8/1,398 (= 0.0397). From inspection of the types of substitutions involved in these changes, R = 267/177 (= 1.5085), $\alpha_1$ = 75/444 (= 0.1689), $\alpha_2$ = 32/444 (= 0.0720), and $\alpha_3$ = 337/444 (= 0.7590). These values were used to estimate character-state weights for heuristic comparison with equal weights in parsimony analysis of nucleotide data (see Table 1).

using selected representatives and outgroups. To be trustworthy, the $\bar{\lambda}$ inferred should be less than ≈0.1, and R should be greater than 1 : 1.

The latter conditions return us to consideration of the number of tree segments. An a priori topology with few segments is expected to give conservative (i.e., relatively even) weight estimates. For example, with increasing phylogenetic depth (e.g., angiosperms analyzed together with *Marchantia* or also with *Chlamydomonas*; Albert et al., 1992), the excess of observable transitions (relative to transversions) becomes lower (probably due to multiple substitutions occurring at the same site despite the mutational bias favoring transitions; cf. Brown et al., 1982; Gojobori et al., 1982; Li et al., 1984), and first and second codon positions accrue larger proportions of total substitutions (many of which are probably amino acid replacement substitutions in contrast to third position "silent" substitutions; Albert et al., 1992; see also Brown et al., 1982).

Despite the restricted number of segments available for estimating effective substitutions and their asymmetries, the "land plant" tree of Albert et al. (1992; Fig. 2) is a robust, a priori topology. Albert et al. (1992) optimized *rbc*L sequence data onto this tree to derive values for use with their restriction-site weighting model. The plastid *rbc*L gene (which encodes the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase) has been sampled extensively for evidence of seed-plant relationships (see Chase et al., 1993, and other papers in this issue). Transformational probabilities and weights that may be relevant to such phylo-

TABLE 1. Character-state weights for *rbc*L sequences based on the "land plant" tree of Albert et al. (1992). State transformation probabilities, $P$, and corresponding character-state weights, $-\ln(P)$, for transition and transversion substitutions in each of the three codon positions, calculated using a priori values from Figure 2 and expressions (4) and (5). Initial weights for use with PAUP 3.0 stepmatrices could be the $-\ln(P)$ rounded to three significant digits and multiplied by $10^3$.

| Substitution type | Codon position | $P$ | $-\ln(P)$ |
|---|---|---|---|
| Transition | 1 | 0.00400751 | 5.51959 |
| | 2 | 0.00171601 | 6.36775 |
| | 3 | 0.0176189 | 4.03878 |
| Transversion | 1 | 0.0013331 | 6.62025 |
| | 2 | 0.000569663 | 7.47047 |
| | 3 | 0.00593453 | 5.12697 |

genetic studies were calculated from expressions (4) and (5) using values obtained from the "land plant" tree (Fig. 2; Table 1). These weights may be designated in three stepmatrices, one assigned to each codon position in *rbc*L. The assumption block format for PAUP 3.0 (Swofford, 1991) is shown for first, second, and third positions, respectively:

```
usertype first = 4
        a       c       g       t
  [a]   —       6620    5520    6620
  [c]   6620    —       6620    5520
  [g]   5520    6620    —       6620
  [t]   6620    5520    6620    —
        ;
usertype second = 4
        a       c       g       t
  [a]   —       7470    6368    7470
  [c]   7470    —       7470    6368
  [g]   6368    7470    —       7470
  [t]   7470    6368    7470    —
        ;
usertype third = 4
        a       c       g       t
  [a]   —       5127    4039    5127
  [c]   5127    —       5127    4039
  [g]   4039    5127    —       5127
  [t]   5127    4039    5127    —
```

In such stepmatrices, the direction of transformation is indicated by [nucleotide] → nucleotide. Differential weighting may begin at the taxon-addition stage or may use starting trees found from prior, equally-weighted Fitch parsimony analyses (both following the recommendations made by Maddison (1991) for discovering all most-parsimonious trees). The latter strategy is significantly less time-consuming: the weights shown above are so close to a 1 : 1 : 1 : 1 assumption that Fitch topologies should include (or lie near) optimal weighted trees. Although this weighting scheme will select specific trees based upon the ad hoc assumptions of the model and the specific values given its parameters, it is useful in identifying neighborhoods of trees (defined by proximity in terms of branch rearrangements) that could provide better hypotheses of the true tree given the empirically observed character and character-state asymmetries. As such, character-state weights derived as above (i.e., Fig. 2; Table 1) should only be considered initial estimates to be supplemented by additional analyses using bracketing values, including equal weighting of character-state transformations (i.e., Fitch parsimony; cf. Albert et al., 1992).

## EXPECTATIONS OF PERFORMANCE: CONSISTENCY UNDER BRANCH-LENGTH ASYMMETRIES AND SENSITIVITY TO TAXON NUMBER

Felsenstein (1978) introduced considerations of statistical consistency for parsimony under the Camin-Sokal (Camin & Sokal, 1965) and Wagner (Farris, 1970; Kluge & Farris, 1969) optimality criteria. His model (a special case of the conditions established by Steel, 1989; Penny et al., 1991) included an unrooted tree of four taxa where two nonadjacent branches of equal length had accumulated much higher numbers of changes than the three others, which were themselves of equal length. A spurious reconstruction in which the taxa with the long branches were grouped because of shared homoplasies was shown to result from unequal rates of character-state change. This phenomenon is better recast in terms of λ because branch lengths (and hence the potential for spurious attraction) are a function of *both* rate and divergence time (Albert et al., 1992; Hendy & Penny, 1989).

Although we do not regard statistical consistency as necessary to justify the use of parsimony (see also Farris, 1983; Sober in Felsenstein & Sober, 1986; Sober, 1988), our previous λ-based heuristic examination of consistency for binary data shows that parsimony analyses *are* generally consistent (under the model specified by Felsenstein, 1978) for data that could be expected to show evidence of common ancestry (Albert et al., 1992). Hendy & Penny (1989) have suggested that breaking up long branches through the addition of appropriate

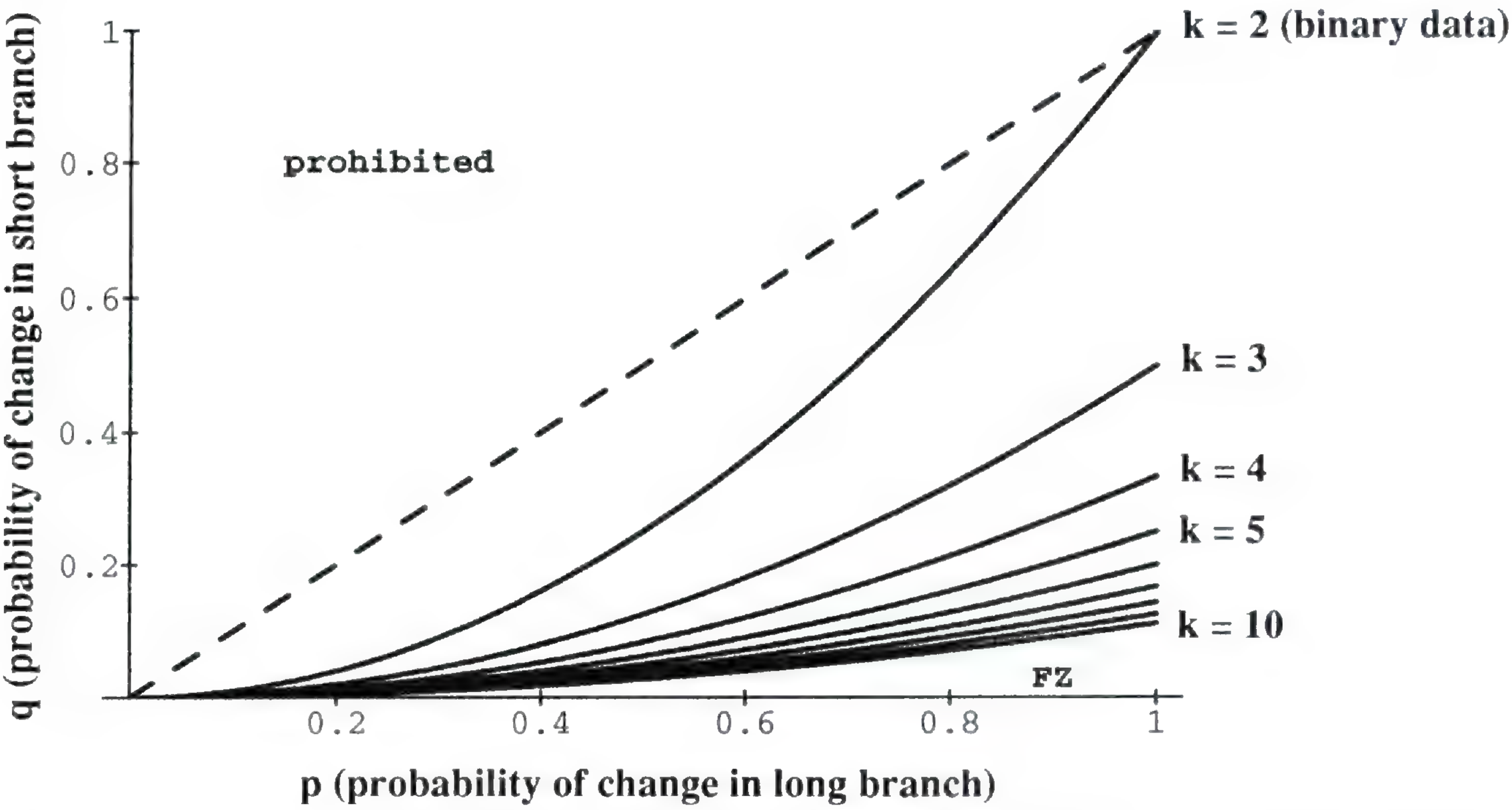



FIGURE 3. The relationship between Felsenstein's consistency model and the number of available character states. Given probabilities $p^2$ (for parallel changes on long, nonadjacent branches) and q (for a change in the same character on the short, connecting branch), the approximation $q > [1/(k - 1)]p^2$ must hold for parsimony to be consistent under Felsenstein's model. The X and Y axes represent p and q probabilities, respectively. By definition, $q > p$ (above the dashed line) is prohibited. Each curve appearing successively below the $q = p$ line represents $[1/(k - 1)]p^2$ for k = 2, 3, 4, 5, 6, 7, 8, 9, and 10. The first curve (for binary data) indicates a relatively large region of inconsistency (the area below; labeled FZ for Felsenstein zone). As the number of character states increases to 4 (as in nucleotide data; the third curve) and then 10 (the last curve), the region of inconsistency decreases dramatically. This behavior is attributable to the lower probability of a parallel change when more states are available. With binary data, q = 0.2 and p = 0.6 would be inconsistent, whereas this asymmetry would be acceptable with nucleotide sequence data.

taxa may permit parsimony to avoid systematic error (cf. Swofford & Olsen, 1990). Nevertheless, Steel (1989) and Penny et al. (1991) underscored that the range of cases where parsimony may be inconsistent increases as the number of taxa increases. Although this may be true, the practical consideration is not so much the absolute number of terminal taxa as an increase in those detracting from the evenness of sampling of the true tree (the shape of which is unknown). Perhaps with real data, the best strategy for limiting the occurrence of long, spuriously connected branches is always to examine many terminal taxa (within computational limits). Nevertheless, sampling considerations apply, such as the range and eccentricity of nucleotide variation being compared (V. A. Albert & K. Bremer, unpublished). Weighting is not expected to affect the frequency of spurious branch attraction greatly because false character-state identity, when it occurs, is an intrinsic and unquantifiable property of the data matrix. Nevertheless, there is heuristic value in comparing the consistency properties of the Fitch criterion with those of parsimony analysis using the present weighting scheme.

## FELSENSTEIN'S CONSISTENCY MODEL

If we imagine two equally long branches connected by a shorter branch to be the "true" topological relationship, avoidance of inconsistency using parsimony (after the model of Felsenstein, 1978) requires that the probability of parallel character-state changes in each of the long branches ($p^2$) be lower than the probability of a single change in the same character occurring in the connecting branch (q). This is expressed by the general approximation $q > [1/(k - 1)]p^2$, where k is the number of character states (J. Felsenstein, pers. comm.). Thus, for binary data, the simple inequality $q > p^2$ must hold (see Albert et al., 1992). For DNA data (k = 4), the approximation is $q > (\frac{1}{3})p^2$ (note that as k increases, $p^2$ becomes smaller; Fig. 3). Thus, $q - [(\frac{1}{3})p^2]$ must be positive for parsimony to be consistent under Felsenstein's model.

Relevant assumptions include (i) a large ($\rightarrow \infty$) random sampling of independent characters whose probabilities of character-state change are equal (see the pertinent objections of Farris, 1983) and (ii) the simplification that both long branches have equal probabilities of change. Assumptions (i) and (ii) are unrealistic in practice, because (i) actual data sets may consist of relatively few, nonrandomly selected characters that may show both interdependence and (ii) asymmetrical probabilities of change. Thus, Felsenstein's model can only approximate consistency behavior for real data.

If we assume a simple Poisson model of nucleotide substitution (as is appropriate for low probabilities of change; cf. Farris, 1973; Felsenstein, 1973; Goldman, 1990; Lanyon, 1988), the probability of a single character-state change in segment interval $T$, $P(T)$, may be estimated by $\lambda e^{-\lambda}$ (note, however, that for $\lambda \ll 1$, $\lambda e^{-\lambda} \approx \lambda$). This formulation ignores the possibility of multiple substitutions, which is an appropriate approximation because two or more changes are improbable at low $\lambda$. For the Fitch model, changes to any different nucleotide are equiprobable. Thus, substituting X for the short-branch $\lambda$ and Y for the long-branch $\lambda$ (as in Albert et al., 1992), the approximate consistency criterion becomes:

$$Xe^{-X} - (\tfrac{1}{3})Y^2e^{-2Y} > 0 \qquad (9)$$

An analysis of this approximation for all X, Y $\leq$ 0.1 demonstrates that a smaller region of inconsistency ("Felsenstein zone"; Fig. 4a) exists than that found for binary characters by Albert et al. (1992). This is explained by the smaller probability of parallel change when more character states are available (see Fig. 3).

The same scenario with four nucleotides can be extended to permit correction for the possibility of multiple substitutions. The expectation is that the Felsenstein zone would shrink because recognition of intermediate substitutions would limit hypotheses of parallel (homoplastic) character-state identities on long branches. Evaluation of this prediction can be accomplished by use of the Jukes-Cantor (J-C) random nucleotide substitution model (Jukes & Cantor, 1969). Using net probabilities of substitution (i.e., the probability of change to any of three potential derived states) during segment interval $T$, the approximate consistency criterion becomes:

$$(\tfrac{3}{4})[1 - e^{-(4/3)X}] - (\tfrac{1}{3})\left((\tfrac{3}{4})[1 - e^{-(4/3)Y}]\right)^2 > 0 \qquad (10)$$

Expression (10) further reduces the size of the Felsenstein zone beyond that observed for expression (9) or for the binary model of Albert et al. (1992; see Fig. 4b).

The K2P model that we use for the present weighting scheme (excluding $\bar{\lambda}\alpha$ partitions) also has an approximate consistency criterion (J. Felsenstein, pers. comm.):

$$[P_{xi}(T);\ X] + 2[P_{xv}(T);\ X] - [P_{xi}(T);\ Y]^2 + 2[P_{xv}(T);\ Y]^2 > 0 \qquad (11)$$

The probabilities indicated are from expressions (4) and (5), and the $1/(k - 1)$ correction for number of states is replaced by multipliers to indicate the two possible transversions from a particular starting nucleotide. Because parallelism on p branches could occur through either transitions or transversions, the consistency criterion must include both possibilities. The expectation is that the Felsenstein zone should be larger at high values of R because this bias would make parallel changes more frequent. When R is close to 1 (see expressions [4] and [5]), the K2P model yields a small realm of inconsistency (at R = 2 it is still smaller than for the J-C model; Fig. 4c). At higher but realistic values of R (e.g., 8) the Felsenstein zone is indeed larger, yet still small enough to permit a wide range of branch-length asymmetries (Fig. 4d).

The net result of this heuristic examination is that consistency itself is not a sufficient justification for favoring one weighting model (the present) over another (Fitch parsimony); the Felsenstein zone is insignificant in all of the scenarios studied. Aside from what this might imply about the necessity for considering consistency (i.e., that it may be irrelevant for justification of parsimony methods), it also suggests that some other factor(s) might have predictive value when comparing the expected performance of weighting models.

## NUMBERS OF TERMINAL TAXA

Breaking up long branches by the addition of more taxa to a data set may be impossible because appropriate taxa may not exist (Hendy & Penny, 1989). Nevertheless, we argue that increasing taxon number can decrease the likelihood of spurious branch attractions (despite the increased number of possibilities where inconsistency could occur; Steel, 1989; Penny et al., 1991) if $\lambda$ values remain relatively small throughout the data. Recall that the number of segments in an unrooted cladogram of $n$ taxa is $[2n - 3 - p]$. Assuming that the number of excess branches at nodes ($p$) remains fairly small for a data set (i.e., not approaching $n$), the number of available segments increases linearly with increasing $n$. Intuitively, one would expect

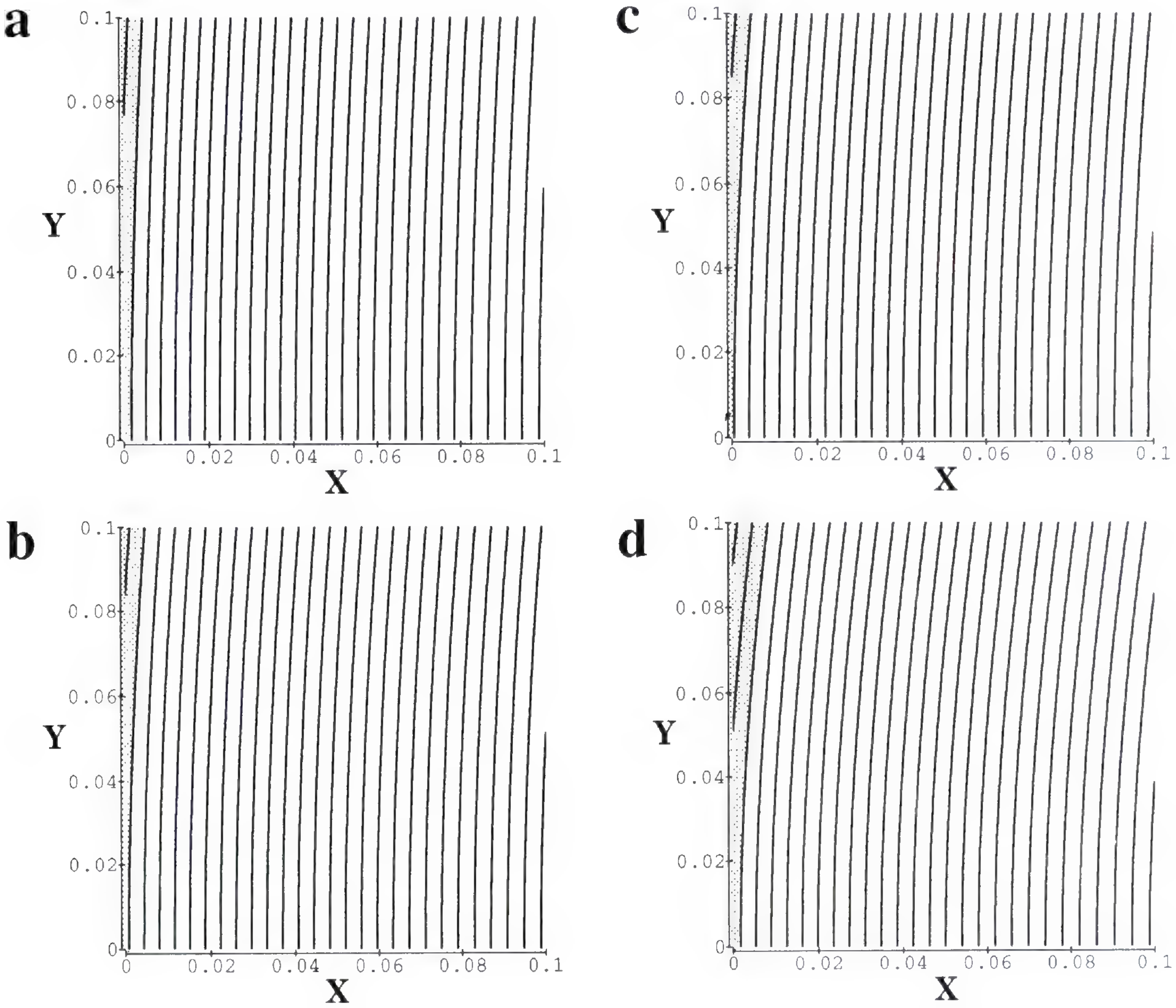



FIGURE 4. Contour plots representing expressions (9–11) for λ values of X and Y between 0 and 1.0, where X is λ for a short branch connecting two long branches with λ values of Y. The approximate region of inconsistency (where X, Y $\lesssim 0$) is shaded (note that the X and Y axes are reversed relative to Fig. 3). Separate plots are shown for the Fitch parsimony model (a), the Jukes-Cantor model (b), and the Kimura 2-parameter model (c: R = 2; d: R = 8). The realm of inconsistency is shown to be miniscule under all models.

Fitch parsimony to provide a more accurate phylogenetic reconstruction if more segments were available for it to discover otherwise hidden "intermediate" substitutions.

Saitou (1989) has formalized this expectation in his analysis of the underestimation of branch lengths by Fitch parsimony. In contrast to the single-state/branch assumption of the Fitch (1971) criterion, Saitou allowed for multiple substitutions (under the J-C model) to account for terminal states on simplified trees with no hierarchical structure (i.e., unresolved polytomies). He found that for all λ values between 0.01 and 1.0, the expected number of required nucleotide changes per branch per site over a tree of $n$ terminal taxa increases as $n$ increases. Saitou's (1989: 5) reasoning for this observation is much the same as for the intuitive example above: ". . . determination of the ancestral nucleotide X becomes more and more unambiguous as $[n]$ is increased, hence more parallel changes are detectable." Saitou also observed that underestimation of branch lengths (λ, under his model) remains small with a relative difference of 6.4% at all reasonable λ values (i.e., $\leq 0.1$; at $\lambda = 0.01$, the difference is only 0.7%). However, at $\lambda = 0.2$, the underestimation is by 12.2%, at $\lambda = 0.5$, 27.0%, and at $\lambda = 1$ (indicative of 1 expected change per character for every tree segment), Fitch parsimony not surprisingly "gives a gross underestimate [by 44.8%] of the branch lengths" (Saitou, 1989: 5). Thus, Saitou's observations independently support the range of λ values (i.e., $\leq$ 0.1) for which the Felsenstein zone was shown to be miniscule (Albert et al., 1992). Additionally, Saitou's calculations (1989, his table 5) suggest that appropriately small estimates of λ (i.e., 0.01

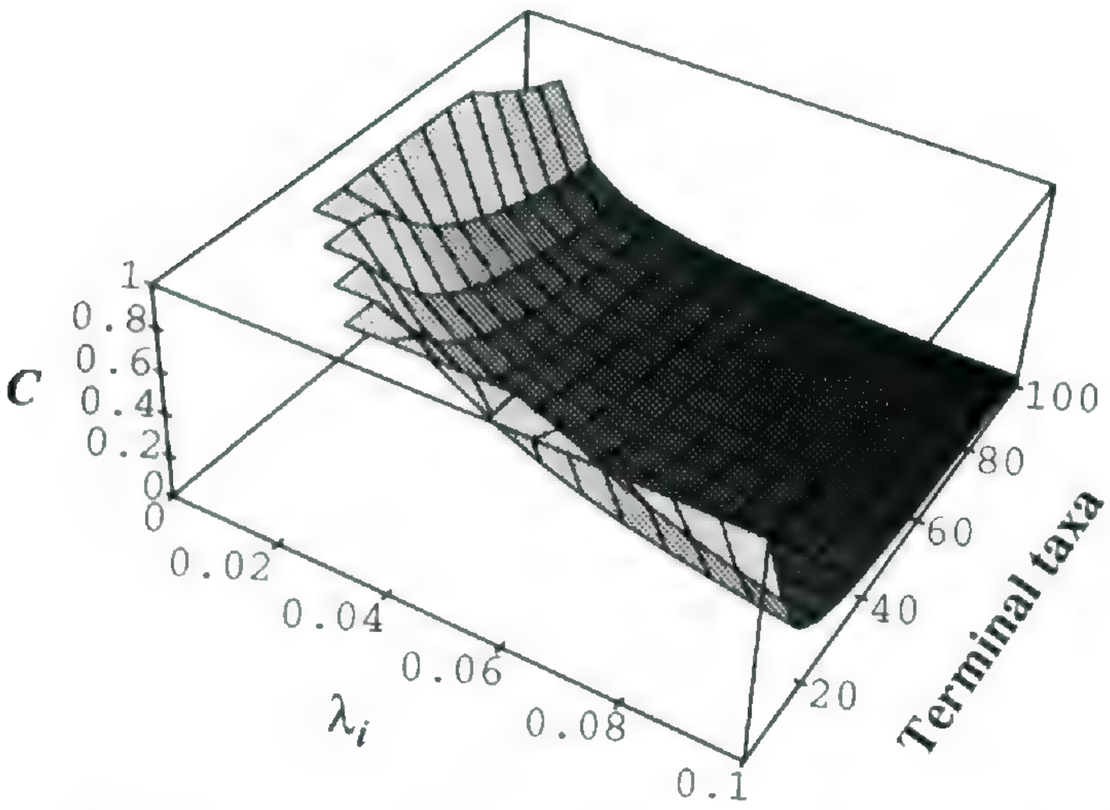
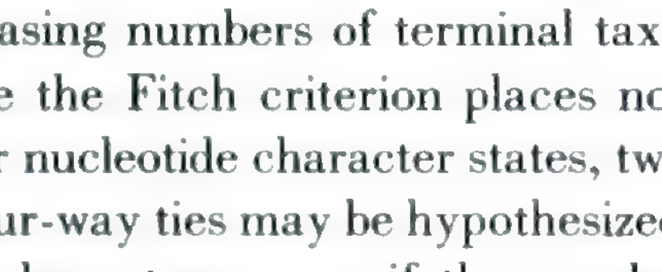



FIGURE 5. Three-dimensional representation of the relationship between the number of taxa, $n$ (X axis), segment length for a given character, $\lambda_i$ (Y axis), and the consistency index, $C$ (Z axis), for binary characters, from expression (14). The behavior of the function, under the simplifying assumption of $\lambda_i$ equality throughout a tree (i.e., $\bar{\lambda}_i$), clearly shows the decrease of $C$ as $\lambda_i$ values and the number of taxa get larger (ranging from 3 to 100). Underlying this behavior is the effect of segment number, here simplified to $[2n - 3]$ for unrooted trees; recall that the number of character-state changes in the $i$th character is, correspondingly, $\lambda_i[2n - 3]$. Only solutions less than or equal to the theoretical maximum of $C$ (1.0) are shown; impossible $n$ and $\lambda_i$ combinations were excluded from the surface.

→ 0.1) should be stable under the Fitch criterion with increasing numbers of terminal taxa.

Because the Fitch criterion places no ordering on the four nucleotide character states, two-, three-, or even four-way ties may be hypothesized at nodes for some characters, even if the number of segments is large. The number of informative nucleotide positions usually differs when analyzing data with equal versus differential character-state weighting. For the Fitch criterion, only putative synapomorphies (e.g., 98 As and two Ts at a particular site in a 100-taxon comparison) can be used to justify most-parsimonious trees. Differential character-state weighting with stepmatrices imposes a partial transformation series among nucleotides. Because transitions and transversions are not given equal weight, state changes between nucleotides are differentially connected:




where $\theta$ indicates the unweighted path between any nucleotide pair, $\upsilon$, the weighted path for a transversion (shown as a bolder line to indicate its higher relative cost), and $\iota$, the weighted path for a transition. For example, a nucleotide position with 98 As, one T, and one C is considered informative for optimization under the present model. Consider a third case: 97 As, two Ts, and one C—the possible pathways between the various A and T states and the single C state are optimized along with all other available data, and the least costly transformations are hypothesized. Such hypotheses might include autapomorphy for C, synapomorphy for the Ts, an A → T → A → T transformation path with C autapomorphous, or even a path including all nucleotide variation, such as A → C → T → A → T. Because of the connectedness provided by weighted paths, what might be ambiguous states at nodes for the Fitch criterion should often be resolved by differential character-state weighting.

Despite (i) the greater proportion of available information used by our differential weighting method and (ii) the arguments given above concerning resolution of multiple substitutions with increased terminal taxa, a methodological caution is in order. Because of the limitations of current software (and available hardware), both the determination of maximum parsimony and the discovery of all most-parsimonious trees are difficult at best with large data sets (e.g., Chase et al., 1993). Therefore, our statements about taxonomic sampling should not be taken as "more is better" for empirical studies; rather, they are intended as logical arguments that may or may not be applicable to real-world scenarios.

## MEASURING CHARACTER-STATE CHANGE: THE CONSISTENCY INDEX IN TERMS OF λ AND NUMBERS OF TERMINAL TAXA

The ensemble consistency index, $C$ (Kluge & Farris, 1969; Farris, 1989a, b, 1991) is a useful measure of homoplasy with respect to a tree. Farris (1989b: 407) described the interpretation of $C$: "The consistency index assesses homoplasy as a fraction of the character change on a tree, and so the frequency with which states arise in parallel." Implicit in Farris's discussion of $C$ is dependence upon the number of terminal taxa in the analysis (as well as characters; Farris, 1989a, b, 1991). We will show that taxon dependence is in turn a function of the number of available tree segments and $\lambda_i$ values for each character. First define (in per-character terms, after Farris, 1989a) $c = m/s$, where $s$ is the number of observed state changes for a given character, and $m$ is the minimum amount of change a character may have on any tree.

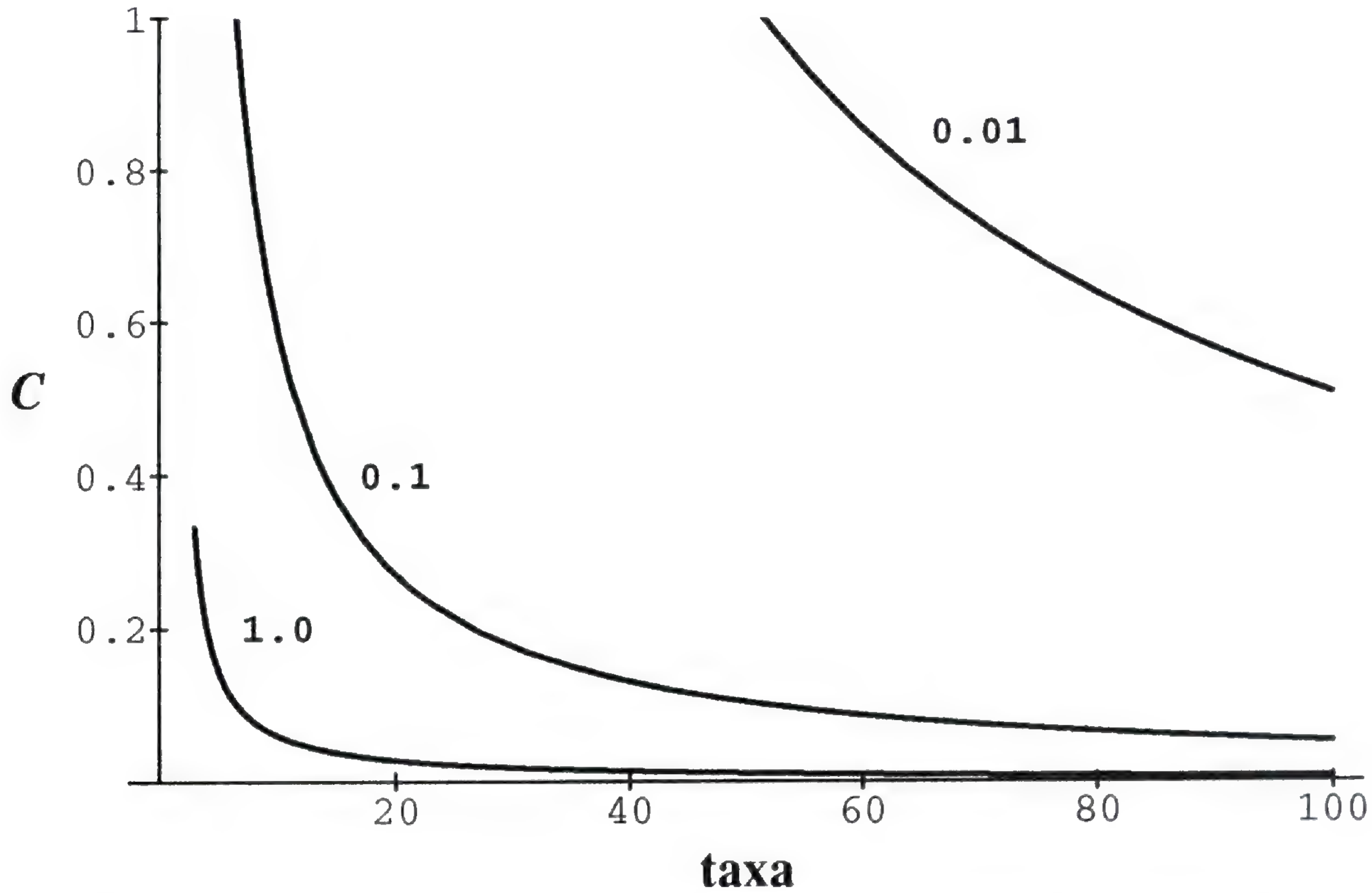



FIGURE 6. Behavior of the consistency index, $C$ (Y axis), under different assumptions of segment length for a given character, $\lambda_i$, and numbers of taxa (X axis), from expression (14). The three curves represent $\lambda_i = 0.01$, 0.1, and 1.0. Under this model for the consistency index, data with $\lambda_i = 1.0$ can never show the absence of homoplasy. This is to be expected because $\lambda_i = 1.0$ implies that $i$ changes state once per tree segment. The curve representing $\lambda_i = 0.1$ shows a behavior evocative of the results of Sanderson & Donoghue (1989), Goloboff (1991), and Klassen et al. (1991); $C$ decreases as the number of taxa (and so tree segments) increases. The $\lambda_i = 0.01$ curve displays a corresponding decrease, but $C = 1.0$ may be reached on trees with far greater numbers of taxa.

Rearranging expression (2) above to solve for $s$ (which is equivalent to $\Delta_i$),

$$s = (\bar{\lambda}_i)[2n - 3 - p] \tag{12}$$

$c$ for the $i$th character can be reformulated as:

$$c = \frac{m}{(\bar{\lambda}_i)[2n - 3 - p]} \tag{13}$$

Thus, ensemble consistency index may be expressed as:

$$C = M \Big/ \left[ \sum_{i=1} (\bar{\lambda}_i)[2n - 3 - p] \right];$$

$$\text{where } M \text{ is } \Sigma_m. \tag{14}$$

Consider the special two-state (binary) case where $m = 1$ and $M$ is equal to the number of variable characters in the data matrix (e.g., conversion of nucleotide data into purines/pyrimidines). Because adding terminal taxa (and so tree segments) increases the denominator in (13) for all possible $\bar{\lambda}_i$/tree-size combinations (i.e., those not violating the theoretical maximum of $c = 1.0$), both individual $c$ values and ensemble $C$ should decrease. A graphic representation of this relationship is shown by the three-dimensional surface in Figure 5; a two-dimensional plot (Fig. 6) highlights the behavior for specific $\bar{\lambda}_i$ values (compare the similar results obtained by Sanderson & Donoghue (1989, fig. 1a), Goloboff (1991, fig. 2a), and Klassen et al. (1991, fig. 3), which were calculated under other premises). Although this effect is seen here with the assumption that $\lambda_i$ values are equal throughout the tree (i.e., through use of $\bar{\lambda}_i$), the above formalization of the effect of increasing taxa and decreasing $C$ should hold for most empirical data (for reasonable $\lambda$s $\leq$ about 0.1, Albert et al., 1992; cf. Sanderson & Donoghue, 1989). Dependence effects based on the number of characters are not readily apparent, other than the implication that more characters means more independent and possibly $\lambda_i$-heterogeneous character-state distributions (among specific terminal taxa) to be considered during an evaluation of maximum parsimony.

## Prospectus

Our prediction of the performance of the character-state weighting model presented here relies on the relationship between numbers of terminal taxa (and so tree segments) and the ability to detect multiple substitutions; both are necessary to estimate λ values on phylogenetic trees. Because our weighting model is intended to provide a correction for multiple substitutions (differentially for each codon position), it should identify better-supported trees than Fitch parsimony for topologies that do not have sufficient numbers of segments for discernment of parallel, backward, and successive multiple-substitution events (cf. Saitou, 1989). The expectation is that analyses of data sets with large and sufficiently even samplings of terminal taxa will converge on the same most-parsimonious topologies (in whole or in part), using either equal or differential character-state weighting. This has been borne out in several studies (e.g., Albert & Chase, unpublished; Qiu et al., 1993). Perhaps indicating inadequate taxon sampling, the weighting method sometimes selects topologies that are slightly less parsimonious under equal weighting (e.g., Clark et al., 1993, in press).

Our conclusion, perhaps paradoxical from the title of this paper, is that our weighting model actually supports the use of the computationally simpler Fitch criterion for DNA sequence data, given adequate taxonomic sampling (see also Albert & Mishler, 1992; Donoghue et al., 1992). Albert et al. (1992) came to identical conclusions with regard to character-state weighting for restriction site data versus Wagner parsimony. Equal weighting of characters may be a strong assumption (see Swofford & Olsen, 1990), but the differential weighting schemes we have examined show that equal weighting is robust to large asymmetries in transformational probabilities among and within characters.

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APPENDIX. Species analyzed in papers published in this issue of the *Annals of the Missouri Botanical Garden*. These are arranged alphabetically by families (dicots according to Cronquist; monocots according to Dahlgren); within families, they are arranged alphabetically by genus.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Acanthus montanus* T. Anderson | Acanthaceae | *Duke Univ. BG s.n.*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L12592 | 15A, B |
| *Aphelandra sinclairana* Nees | Acanthaceae | *Uppsala BG 0000-3212*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L01884 | 15A, B |
| *Barleria prionitis* L. | Acanthaceae | *Uppsala BG 1977-3036*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L01886 | 15A, B |
| *Hypoëstes forsskaolii* R. Br. | Acanthaceae | *Ensermu Kelbessa s.n.*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L12593 | 15A, B |
| *Justicia americana* (L.) Vahl | Acanthaceae | *Olmstead 90-011*, COLO | 27-745, 753-957, 965-1428 | Olmstead et al., 1993 | L14401 | 15A |
| *Justicia odora* (Forssk.) Lam. | Acanthaceae | *Hedrén et al. 746*, UPS | 29-1428 | Albert et al., 1992b (Hedrén) | L01930 | 15A, B |
| *Lepidogathis villosa* Hedrén | Acanthaceae | *Thulin et al. 7728*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L12594 | 15A, B |
| *Phaulopsis* sp. nov. | Acanthaceae | *Steiner & Manktelow 32*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | | 15A |
| *Ruellia graecizans* Backer | Acanthaceae | *Uppsala BG 1957-3039*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L12595 | 15A, B |
| *Ruttya fruticosa* Lindau | Acanthaceae | *Uppsala BG 1977-3070*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L02434 | 15A, B |
| *Thunbergia usambarica* Lindau | Acanthaceae | *Uppsala BG 1984-3474*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L12596 | 15A, B |
| *Acer saccharum* L. | Aceraceae | *M. W. Chase 106*, NCU | 31-1428 | Albert et al., 1992b (Chase) | L01881 | 10A, B, 16 |
| *Actinidia chinensis* Planch. | Actinidiaceae | *Kron 2117*, NCU | 31-1428 | Albert et al., 1992b (Kron) | L01882 | 13A, B |
| *Adoxa moschatellina* L. | Adoxaceae | *Donoghue et al. 1*, WISC | 27-1428 | Donoghue et al., 1992 | L01884 | 14A, B |
| *Agave* sp. | Agavaceae | unknown | 32-1350 | Duvall et al, 1993 (Eguiarte) | | |
| *Beschornia* sp. | Agavaceae | unknown | 32-1350 | Duvall et al, 1993 (Eguiarte) | | |
| *Heperaloe* sp. | Agavaceae | unknown | 32-1350 | Duvall et al, 1993 (Eguiarte) | | |
| *Manfreda* sp. | Agavaceae | unknown | 32-1350 | Duvall et al, 1993 (Eguiarte) | | |
| *Yucca* sp. | Agavaceae | unknown | 32-1327 | Duvall et al, 1993 (Eguiarte) | | |
| *Trianthema portulacastrum* L. | Aizoaceae | *Rettig s.n.*, TAMU | 1-1428 | Rettig et al., 1992 | M62572 | 9A, B |
| *Akania bidwillii* (Hogg) Mabb. | Akaniaceae | *Fernando & Quinn 21606*, UNSW | 19-1428 | Gadek et al., 1992 | L12568 | 10B |
| *Alangium chinense* (Lour.) Harms | Alangiaceae | U.S. Natl. Arb. 49003 | 31-1407 | Xiang et al., 1993 | L11209 | 12A, B |
| *Alisma plantago-aquatica* L. | Alismataceae | *Les s.n.*, CONN | 29-1183 | Chase et al., 1993 (Les) | L08759 | 5A, B |
| *Sagittaria graminea* v. *chapmannii* J. G. Sm. | Alismataceae | *M. W. Chase 210*, NCU | 27-1208 | Chase et al., 1993 (Chase) | | 5A, B |
| *Sagittaria latifolia* Willd. | Alismataceae | *Les s.n.*, CONN | 29-1183 | Chase et al., 1993 (Les) | L08767 | 5A, B |
| *Alstroemeria* sp. | Alstroemeriaceae | *W. R. Anderson 13653*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Amaranthus hypochondriacus* L. | Amaranthaceae | unknown | 1-1428 | Michalowski et al., 1990 | X51964 | 9A, B |
| *Clivia miniata* Regel | Amaryllidaceae | *Bradley 24976*, GMUF | 32-1351 | Duvall et al., 1993 (Duvall) | L05032 | 5A, B |
| *Amborella trichopoda* Baill. | Amborellaceae | *Thien 500*, NO | 29-1428 | Qiu et al., 1993 | L12628 | 4A, B |
| *Schinus* sp. | Anacardiaceae | *W. R. Anderson 13601*, MICH | 29-1428 | Chase et al., 1993 (Chase) | | 10A, B, 16 |
| *Annona muricata* L. | Annonaceae | *Qiu 90031*, NCU | 29-1428 | Qiu et al., 1993 | L12629 | 4A, B |
| *Asimina triloba* (L.) Dunal | Annonaceae | *Qiu 15*, NCU | 29-1428 | Qiu et al., 1993 | L12631 | 4A, B |
| *Cananga odorata* (Lam.) Hook. f. & Thomson | Annonaceae | *M. W. Chase 219*, NCU | 27-1351 | Qiu et al., 1993 | L12636 | 4B |
| *Chlorophytum comosum* Baker | Anthericaceae | *Bradley 7331*, GMUF | 32-1351 | Duvall et al., 1993 (Duvall) | L05031 | 5A, B |
| *Apium graveolens* L. | Apiaceae | *Plunkett 1334*, WS | 31-1407 | Albert et al., 1992b (Plunkett & Soltis) | L01885 | 14A, B |
| *Conium maculatum* L. | Apiaceae | *Plunkett 1266*, WS | 31-1407 | Chase et al., 1993 (Plunkett & Soltis) | L11167 | 14A |
| *Coriandrum sativum* L. | Apiaceae | none | 103-1428 | Olmstead et al., 1992 | L11676 | 14A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Sanicula gregari* Bicknell | Apiaceae | *Ware 9898*, WILLI | 31-1407 | Chase et al., 1993 (Plunkett & Soltis) | L11170 | 14A, B |
| *Apocynum cannabinum* L. | Apocynaceae | none | 103-1428 | Olmstead et al., 1992 | L11678 | 15A, B |
| *Kopsia fruticosa* DC. | Apocynaceae | *B. Bremer 3033*, UPS | 128-1434 | Olmstead et al., 1993 | L14402 | |
| *Ilex crenata* Thunb. | Aquifoliaceae | *M. W. Chase 119*, NCU | 31-1428 | Albert et al., 1992b (Chase) | L01928 | 14A, B |
| *Ilex vomitoria* Aiton | Aquifoliaceae | *Rettig 1660*, TAMU | 1-1407 | Chase et al., 1993 (Rettig) | M88583 | 14A |
| *Acorus calamus* L. | Araceae | *French 232*, CH | 29-1270, 1319-1352 | Duvall et al. 1993 (Duvall) | M901625 | 5B |
| *Gymnostachys anceps* R. Br. | Araceae | *Howard 4325*, FTG | 32-1404 | Duvall et al. 1993 (Duvall) | M91629 | 5A, B |
| *Lemna minuscula* Herter | Araceae | *Duvall 19920501*, UCR | 32-1351 | Duvall et al. 1993 (Duvall) | M91630 | 5B |
| *Pistia stratiotes* L. | Araceae | *French 233*, CH | 31-1351 | Duvall et al. 1993 (Duvall) | M96963 | 5B |
| *Spathiphyllum wallisii* Hort | Araceae | *M. W. Chase 210*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Aralia spinosa* L. | Araliaceae | *Plunkett 1371*, WS | 31-1407 | Chase et al., 1993 (Plunkett & Soltis) | L11166 | 14A, B |
| *Diplopanax stachyanthus* Hand.-Mazz. | Araliaceae | *Jin-hua 1*, NH | 31-1407 | Xiang et al., 1993 | L11224 | 12A, B |
| *Hedera helix* L. | Araliaceae | *Jansen s.n.*, MICH | 27-1428 | Olmstead et al. 1992 | L01924 | 14A, B |
| *Calamus usitatus* Mart. | Arecaceae | none | 467-1401 | Gaut et al., 1992 | M81810 | 6A |
| *Caryota mitis* Lour. | Arecaceae | none | 1-1428 | Gaut et al., 1992 | M81811 | 6A |
| *Chamaedorea costaricana* Oerst. | Arecaceae | none | 1-1224 | Gaut et al., 1992 | | 6A, B |
| *Drymophloeus subdistichus* (H. E. Moore) H. E. Moore | Arecaceae | none | 1-1404 | Gaut et al., 1992 | M81812 | 6A, B |
| *Nypa fruticans* Wurb. | Arecaceae | none | 31-1404 | Gaut et al., 1992 | M81813 | 6A, B |
| *Phoenix reclinita* Jacq. | Arecaceae | none | 1-1401 | Gaut et al., 1992 | M81814 | 6A |
| *Serenoa repens* (Bartram) Small | Arecaceae | none | 1-1401 | Gaut et al., 1992 | M81815 | 6A, B |
| *Aristolochia macrophylla* Lam. | Aristolochiaceae | *Qiu 91019*, NCU | 29-1428 | Qui et al., 1993 | L12630 | 4A, B |
| *Asarum canadense* L. | Aristolochiaceae | none | 27-1428 | Chase et al., 1993 (Olmstead) | L14290 | 4A, B |
| *Saruma henryi* Oliv. | Aristolochiaceae | *Qui 91018*, NCU | 29-1428 | Qiu et al., 1993 | L12664 | 4A, B |
| *Asclepias exaltata* L. | Asclepiadaceae | *Olmstead 88-010*, COLO | 103-881, 888-1428 | Olmstead et al., 1993 | L14390 | 15A, B |
| *Asparagus officinalis* L. | Asparagaceae | *Duvall 19920604*, UCR | 32-1351 | Duvall et al., 1993 (Duvall) | L05028 | |
| *Aloe vera* (L.) Burm. | Asphodelaceae | *Bradley 24977*, GMUF | 32-1351 | Duvall et al., 1993 (Duvall) | L05029 | 5A, B |
| *Haworthia subfasciata* Baker | Asphodelaceae | *Bradley 24978*, GMUF | 32-1351 | Duvall et al., 1993 (Duvall) | L05035 | 5A, B |
| *Kniphofia uvaria* (L.) Hook. | Asphodelaceae | *M. W. Chase 120*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Achillea millefolium* L. | Asteraceae | *Jansen 911*, MICH | 1-1428 | Kim et al., 1992 | L13641 | 14A, B |
| *Barnadesia carophylla* (Vell.) S. F. Blake | Asteraceae | *Jansen 907*, MICH | 1-1428 | Kim et al., 1992 (Michaels) | L13859 | 14A |
| *Blennosperma nana* (Hook.) S. F. Blake | Asteraceae | *Ornduff 8739*, UC | 1-1428 | Kim et al., 1992 | L13645 | 14A |
| *Carthamnus tinctorius* L. | Asteraceae | *USDA P1198990*, MICH | 1-1428 | Kim et al., 1992 (Michaels) | L13862 | 14A, B |
| *Cichorium intybus* L. | Asteraceae | *Jansen s.n.*, MICH | 1-1428 | Kim et al., 1992 | L13652 | 14A, B |
| *Chromolaena* sp. | Asteraceae | *Dillon 4105*, F | 1-1428 | Kim et al., 1992 | L13640 | 14A, B |
| *Chrysanthemum maximum* Ramond | Asteraceae | *Jansen 1000*, MICH | 1-1428 | Kim et al., 1992 | L13648 | 14A |
| *Cacosmia rugosa* Kunth | Asteraceae | *Dillon 4043*, F | 1-1428 | Kim et al., 1992 | L13644 | 14A, B |
| *Coreopsis grandiflora* Hogg. | Asteraceae | *E. Smith 3738*, UARK | 1-1428 | Kim et al., 1992 | L13642 | 14A |
| *Dasyphyllum dicanthoides* (Less) Cabrera | Asteraceae | none | 1-1428 | Kim et al., 1992 (Michaels) | L13863 | 14A |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Dimorphotheca pluvialis* L. | Asteraceae | *Jansen 902*, MICH | 1-1428 | Kim et al., 1992 | L13636 | 14A, B |
| *Echinops exaltata* Koch | Asteraceae | *Jansen 1001*, MICH | 1-1428 | Kim et al., 1992 | L13650 | 14A |
| *Eupatorium atrorubens* G. Nicholson | Asteraceae | *Jansen 908*, MICH | 1-1428 | Kim et al., 1992 | L13649 | 14A |
| *Felicia bergeriana* O. Hoffm. ex Zahlbr. | Asteraceae | *Jansen 996*, MICH | 1-1428 | Kim et al., 1992 | L13639 | 14A, B |
| *Flaveria trinerva* (Spreng.) C. Mohr | Asteraceae | unknown | 1-1428 | Hudson et al., 1990 | | 14A |
| *Gazania splendens* Moore | Asteraceae | *Jansen 912*, MICH | 1-1428 | Kim et al., 1992 | L13638 | 14A |
| *Gerbera jamesonii* Bolus | Asteraceae | *Jansen 915*, MICH | 1-1428 | Kim et al., 1992 | L13643 | 14A, B |
| *Helianthus annuus* L. | Asteraceae | *Price HA 89*, TAES | 1-1428 | Kim et al., 1992 (Michaels) | L13929 | 14A |
| *Lactuca sativa* L. | Asteraceae | none | 1-1428 | Kim et al., 1992 (Michaels) | | 14A |
| *Piptocarpha axillaris* Baker | Asteraceae | *G. Smith 1105*, GA | 1-1428 | Kim et al., 1992 | L13651 | 14A, B |
| *Senecio mikanioides* Otto | Asteraceae | *Missouri BG 72326*, MO | 1-1428 | Kim et al., 1992 (Michaels) | L13933 | 14A, B |
| *Stokesia laevis* (Hill) E. Greene | Asteraceae | *Jansen s.n.*, MICH | 1-1428 | Kim et al., 1992 | L13076 | 14A |
| *Tagetes erecta* L. | Asteraceae | *Jansen 905*, MICH | 1-1428 | Kim et al., 1992 | L13637 | 14A, B |
| *Tragopogon porrifolius* L. | Asteraceae | *Jansen s.n.*, MICH | 1-1428 | Kim et al., 1992 | L13647 | 14A, B |
| *Vernonia mespilifolia* Less. | Asteraceae | *Jansen 995*, MICH | 1-1428 | Kim et al., 1992 | L13646 | 14A, B |
| *Austrobaileya scandens* C. T. White | Austrobaileyaceae | *Qiu 90030*, NCU | 29-1428 | Qiu et al., 1993 | L12632 | 4A, B |
| *Impatiens capensis* Meerb. | Balsaminaceae | *M. W. Chase 114*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 13A, B |
| *Barclaya longifolia* Wall. | Barclayaceae | *Les s.n.*, CONN | 29-1183 | Les et al., 1991 | M77027 | 4A, B |
| *Basella alba* L. | Basellaceae | *Wilson s.n.*, TAMU | 1-1407 | Rettig et al., 1992 | M62564 | 9A, B |
| *Batis maritima* L. | Bataceae | *Rettig 1658*, TAMU | 1-1428 | Chase et al., 1993 (Rettig) | M88341 | 10A, B |
| *Begonia metallica* × *sanguinea* | Begoniaceae | *M. W. Chase 225*, NCU | 27-1351 | Albert et al., 1992b (Chase) | L01888 | 11B, 16 |
| *Caulophyllum thalictroides* (L.) Michx. | Berberidaceae | *Les s.n.*, CONN | 29-1183 | Chase et al., 1993 (Les) | L08760 | 7A, B, 16 |
| *Mahonia bealei* (Fortune) Carr. | Berberidaceae | *Qiu 74*, NCU | 29-1428 | Qiu et al., 1993 | L12657 | 7A, B, 16 |
| *Betula nigra* L. | Betulaceae | *M. W. Chase 255*, NCU | 27-1428 | Albert et al., 1992b (Qiu) | L01889 | 11B, 16 |
| *Catalpa* sp. | Bignoniaceae | *dePamphilis s.n.*, COLO | 103-1428 | Olmstead et al., 1992 | L11679 | 15A, B |
| *Bombax buonopozense* P. Beauv. | Bombacaceae | *Alverson s.n.*, WIS | 27-1428 | Chase et al., 1993 (Karol) | | 10B |
| *Borago officinalis* L. | Boraginaceae | none | 103-1428 | Olmstead et al., 1992 | L11680 | 15A, B |
| *Heliotropium arborescens* L. | Boraginaceae | Matthaei BG 870209 (U Michigan) | 103-1428 | Olmstead et al., 1993 | L14399 | 15A, B |
| *Brassica campestris* L. | Brassicaceae | unknown | 1-1428 | Olmstead et al., 1992 (Nugent & Palmer) | | 10A, B |
| *Stanleya pinnata* (Pursh) Britton | Brassicaceae | *Price s.n.*, IND | 27-1428 | Chase et al., 1993 (Price & Rodman) | | 11B |
| *Bretschneidera sinensis* Hemsl. | Bretschneideraceae | *Leu & Lin 726*, WIS | 27-1428 | Chase et al., 1993 (Rodman) | M95753 | 10B |
| *Aechmea chantinii* (Carrière) Baker | Bromeliaceae | unknown | 1-1428 | Duvall et al., 1993 (Clark) | | 6A |
| *Ananas comosus* (L.) Merrill | Bromeliaceae | unknown | 1-1401 | Duvall et al., 1993 (Clark) | | 6A, B |
| *Catopsis* sp. | Bromeliaceae | unknown | 73-439, 490-1404 | Duvall et al., 1993 (Clark) | | 6A |
| *Glomeropitcairnia* sp. | Bromeliaceae | unknown | 77-415, 450-1404 | Duvall et al., 1993 (Clark) | | 6A |
| *Hechtia montana* Brandegee | Bromeliaceae | unknown | 47-1404 | Duvall et al., 1993 (Clark) | | 6A |
| *Puya dyckioides* (Baker) Mez | Bromeliaceae | unknown | 1-1404 | Duvall et al., 1993 (Clark) | | 6A, B |
| *Tillandsia* sp. | Bromeliaceae | unknown | 1-1428 | Duvall et al., 1993 (Clark) | | 6A, B |
| *Berzelia lanuginosa* (L.) Brongn. | Bruniaceae | *Price s.n.*, IND | 27-1428 | Olmstead et al., 1993 (Price) | L14391 | 14A, B |
| *Buddleja davidii* Franch. | Buddlejacaeae | *Olmstead 88-007*, COLO | 103-1428 | Olmstead et al., 1993 | L14392 | 15A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Nicodemia diversifolia* (M. Vahl) Ten. | Buddlejacaeae | *B. Bremer 3099*, UPS | 27-1434 | Olmstead et al., 1993 | L14413 | |
| *Burmannia biflora* L. | Burmanniaceae | *M. W. Chase 157*, NCU | 30-1428 | Olmstead et al., 1992 (Chase) | | 5A |
| *Bursera inaguensis* Britton | Burseraceae | Fairchild Trop. G FG64-418B | 30-1428 | Albert et al., 1992b (Chase) | L01890 | 10A, B, 16 |
| *Pachysandra procumbens* Michx. | Buxaceae | *M. W. Chase 207*, NCU | 58-1360 | Chase et al. 1993b (Chase) | | 7B, 16 |
| *Byblis liniflora* Salisb. | Byblidaceae | none | 29-1351 | Albert et al., 1992b (Chase) | L01891 | 15B |
| *Roridula gorgonias* Planchon | Byblidaceae | *Goldblatt 5393*, MO | 31-1407 | Albert et al., 1992 (Morgan & Soltis) | L01950 | 13A, B |
| *Brasenia schreberi* J. F. Gmelin in L. | Cabombaceae | *Les s.n.*, CONN | 27-1209 | Les et al., 1991 | M77028 | 4A, B |
| | | *Qui 91031*, NCU | 1210-1428 | Qiu et al., 1993 | | |
| *Cabomba caroliniana* A. Gray | Cabombaceae | *Les s.n.*, CONN | 27-1428 | Les et al., 1991 | M77029 | 4A, B |
| *Callitriche heterophylla* Pursh. emend Darby | Callitrichaceae | *Philbrick 2152*, CONN | 103-1428 | Olmstead et al., 1992 | L11681 | 15A, B |
| *Calochortus minimus* Ownbey | Calochortaceae | *Ness 606*, PUA | 27-1428 | Chase et al., 1993 (Chase) | | 5B |
| *Calycanthus chinensis* Cheng & S. T. Chang | Calycanthaceae | *Qiu 90010*, NCU | 29-1428 | Qiu et al., 1993 | L12635 | 4A, B |
| *Calycanthus floridus* L. | Calycanthaceae | Matthaei BG 810087 (U Michigan) | 27-1428 | Chase et al., 1993 (Olmstead) | L14291 | 4A |
| *Chimonanthus praecox* (L.) Link | Calycanthaceae | *Qiu 62*, NCU | 29-1428 | Qui et al., 1993 | L12639 | 4A, B |
| *Boöpis anthemoides* Juss. | Calyceraceae | *Hunziker 25258*, COLO | 1-377, 432-1428 | Olmstead et al., 1993 (Michaels) | L13860 | 14A, B |
| *Campanula ramulosa* Wall. | Campanulaceae | *Jansen 984*, MICH | 1-1428 | Olmstead et al., 1992 (Michaels) | L13861 | 14A, B |
| *Lobelia erinus* L. | Campanulaceae | *Jansen 989*, MICH | 27-1428 | Albert et al., 1992b (Michaels) | L01931 | 14A, B |
| *Canella winteriana* (L.) Gaertn. | Canellaceae | *Qiu 90017*, NCU | 29-1428 | Qiu et al., 1993 | | 4A, B |
| *Humulus lupulus* L. | Cannabaceae | *Qiu 92004*, NCU | 27-1428 | Chase et al., 1993 (Qiu) | | 11B, 16 |
| *Canna indica* L. | Cannaceae | *Kress 80-1124*, US | 31-1374 | Smith et al., 1993 | L05445 | |
| *Canna tuerkheimii* Kraenzl. | Cannaceae | *Kress 76-653*, US | 31-1374 | Smith et al., 1993 | L05446 | |
| *Capparis hastata* Jacq. | Capparaceae | *Iltis 30315*, WIS | 27-1428 | Rodman et al., 1993 | M95754 | 10A, B |
| *Cleome hasleriana* Chodat | Capparaceae | *Al-Shehbaz s.n.*, MO | 27-1428 | Rodman et al., 1993 | M95755 | 10B |
| *Koeberlinia spinosa* Zucc. | Capparaceae | *Al-Shehbaz s.n.*, MO | 27-1428 | Rodman et al., 1993 | L14600 | 10B |
| *Setchellanthus caeruleus* Brandegee | Capparaceae | *Iltis & Lasseigue 100*, WIS | 27-1428 | Chase et al., 1993 (Karol) | | 10B |
| *Sambucus racemosa* L. | Caprifoliaceae | unknown | 103-1274 | Donoghue et al., 1992 | L14066 | 14A, B |
| *Symphoricarpos albus* (L.) Blake | Caprifoliaceae | *Olmstead s.n.*, COLO | 103-1428 | Olmstead et al., 1992 | L11682 | 14A, B |
| *Viburnum acerifolia* L. | Caprifoliaceae | *Jansen 910*, MICH | 1-1428 | Olmstead et al., 1992 (Michaels) | L01959 | 14A, B |
| *Carica papaya* L. | Caricaceae | Wisconsin BG | 27-1428 | Rodman et al., 1993 | M95671 | 10A, B |
| *Dianthus caryophyllus* L. | Caryophyllaceae | unknown | 1-1407 | Giannasi et al., 1992 | M77699 | 9A, B |
| *Casuarina litorea* L. | Casuarinaceae | *M. W. Chase 215*, NCU | 27-1428 | Albert et al., 1992b (Chase) | L01893 | 11A, B, 16 |
| *Euonymus alatus* (Thunb.) Siebold | Celastraceae | *M. W. Chase 137*, NCU | 27-1428 | Chase et al., 1993 (Chase) | L13184 | 11A, B |
| *Cephalotus folicularis* Labill. | Cephalotaceae | *M. W. Chase 147*, NCU | 31-1407 | Albert et al., 1992b (Morgan & Soltis) | L01894 | 11A, C |
| *Cephalotaxus drupacea* Siebold & Zucc. | Cephalotaxaceae | UC Berkeley BG | 27-1351 | Chase et al., 1993 (Price) | | 3B |
| *Ceratophyllum demersum* L. | Ceratophyllaceae | *Les s.n.*, CONN | 29-1183 | Les et al., 1991 | M77030 | 1–4A, B |
| | | *Qiu 91027*, NCU | 1184-1428 | Qiu et al., 1993 | | |
| *Cerdiciphyllum japonicum* Seibold & Zucc. | Cercidiphyllaceae | *Olmstead 90-016*, COLO | 27-1428 | Olmstead et al., 1992 | L11673 | 8A, B |
| *Atriplex patula* L. | Chenopodiaceae | unknown | 1-1428 | Hudson et al., 1990 | X15925 | 9A, B |
| *Spinacia oleracea* L. | Chenopodiaceae | unknown | 1-1428 | Zurawski et al., 1981 | J01443 | 9A, B |
| *Chloranthus japonicus* Siebold | Chloranthaceae | *M. W. Chase 204*, NCU | 29-1428 | Qiu et al., 1993 | L12640 | 4A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Hedyosmum arborescens* Sw. | Chloranthaceae | *M. W. Chase 338*, NCU | 27-1428 | Qiu et al., 1993 | L12649 | 4B |
| *Sarcandra grandifolia* (Miq.) Subr. & Henry | Chloranthaceae | *Qiu 92002*, NCU | 27-1351 | Qiu et al., 1993 | L12663 | 4B |
| *Chrysobalanus icaco* L. | Chrysobalanaceae | *Fairchild Trop. G 76-311* | 31-1407 | Morgan & Soltis, 1993 | L11178 | 11A, B |
| *Licania tomentosa* Fritsch | Chrysobalanaceae | *Fairchild Trop. G 64-734* | 31-1407 | Morgan & Soltis, 1993 | L11193 | 11A, B |
| *Clethra alnifolia* L. | Clethraceae | *Kron 1884*, NCU | 31-1428 | Kron & Chase, 1993 | L12609 | 13A, B |
| *Burchardia umbellata* R. Br. | Colchicaceae | *M. W. Chase 184*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Colchicum speciosum* Stev. | Colchicaceae | *M. W. Chase 109*, NCU | 31-1428 | Albert et al., 1992a (Chase) | L12673 | 5A, B |
| *Quisqualis indica* L. | Combretaceae | *W. R. Anderson s.n*, MICH | 31-1428 | Albert et al., 1992b (Chase) | L01948 | 10A, 11C |
| *Terminalia catappa* L. | Combretaceae | *Conti 1003*, WIS | 1-1428 | Chase et al., 1993 (Conti) | | 11C |
| *Commelina benghalensis* L. | Commelinaceae | *Duvall 19920603*, UCR | 33-1391 | Duvall et al., 1993 (Duvall) | L05033 | 6B |
| *Tradescantia soconuscana* Matuda | Commelinaceae | *Faden 76-98*, US | 31-277, 309-681, 689-1397 | Smith et al., 1993 | L05463 | 6A, B |
| *Tradescantia* aff. *pallida* | Commelinaceae | *Bradely 24980*, GMUF | 32-1398 | Duvall et al., 1993 (Duvall) | L05041 | 6A, B |
| *Tradescantia zebrina* Bosse | Commelinaceae | *J. Cortesi 7324*, GMUF | 32-1366 | Duvall et al., 1993 (Duvall) | L05042 | 6A, B |
| *Convolvulus tricolor* L. | Convolvulaceae | none | 103-1428 | Olmstead et al., 1992 | L11683 | 15A, B |
| *Ipomoea coccinea* L. | Convolvulaceae | *Olmstead 88-015*, COLO | 103-1274 | Olmstead et al., 1993 | L14400 | 15A, B |
| *Coriaria myrtifolia* L. | Coriariaceae | *M. W. Chase 245*, NCU | 26-1428 | Albert et al., 1992b (Qiu) | L01897 | 11B, 16 |
| *Aucuba japonica* Thunb. | Cornaceae | U.S. Natl. Arb. | 31-1407 | Xiang et al., 1993 | L11210 | 15A, B, 16 |
| *Cornus alternifolia* L. | Cornaceae | *Xiang 167*, WS | 31-1407 | Xiang et al., 1993 | L11212 | |
| *Cornus canadensis* L. | Cornaceae | *Xiang 198*, WS | 31-1407 | Albert et al., 1992b (Xiang) | L01898 | 12A, B |
| *Cornus chinensis* Wangerin | Cornaceae | *Qi-Xing* Aug 1990 | 31-1407 | Xiang et al., 1993 | L11214 | |
| *Cornus florida* L. | Cornaceae | *Xiang 250*, WS | 31-1407 | Xiang et al., 1993 | L11215 | 12A, B |
| *Cornus kousa* Hance | Cornaceae | none | 27-1428 | Olmstead et al., 1993 | L14395 | 12A, B |
| *Cornus mas* L. | Cornaceae | Arnold Arb. 748-75 | 31-1407 | Xiang et al., 1993 | L11216 | 12A |
| *Cornus obliqua* Raf. | Cornaceae | *Xiang 173*, WS | 31-1407 | Xiang et al., 1993 | L11217 | |
| *Cornus oblonga* Wall. | Cornaceae | Kunming BG, China | 31-1407 | Xiang et al., 1993 | L11218 | |
| *Cornus officinalis* Siebold & Zucc. | Cornaceae | Arnold Arb. 8156-A | 31-1407 | Xiang et al., 1993 | L11219 | |
| *Cornus walteri* Wangerin | Cornaceae | Arnold Arb. 414-67-A | 31-1407 | Xiang et al., 1993 | L11220 | 12A, B |
| *Corokia cotoneaster* Raoul | Cornaceae | Strybing Arb. 74-211 | 31-1407 | Xiang et al., 1993 | L11221 | 14A, B |
| *Curtisia dentata* (Burm.) G. A. Sm. | Cornaceae | *Edwards 918*, NU | 31-1407 | Xiang et al., 1993 | L11222 | |
| *Griselinia lucida* G. Forst. | Cornaceae | *Cameron s.n.*, AKU | 31-1407 | Xiang et al., 1993 | L11225 | 14A, B |
| *Helwingia japonica* (Thunb.) F. Dietr. | Cornaceae | Arnold Arb. 912 | 31-1407 | Xiang et al., 1993 | L11226 | 14A, B |
| *Mastixia caudatilimba* C. Y. Wu ex Soong | Cornaceae | *Zan-he s.n.*, WS | 31-1407 | Xiang et al., 1993 | L11227 | |
| *Costus barbatus* Suess. | Costaceae | *Marie Selby BG 86-0550*, SEL | 31-1374 | Smith et al., 1993 | L05447 | 6A, B |
| *Monocostus uniflorus* (Poepp. ex Petersen) Maas | Costaceae | *Kress 79-1112*, SEL | 31-1374 | Smith et al., 1993 | L05454 | |
| *Tapeinochilos ananassae* K. Schum. | Costaceae | *Kress 79-1114*, ? | 31-1374 | Smith et al., 1993 | L05462 | 6A, B |
| *Crassula marnierana* Huber & Jacobsen | Crassulaceae | *Morgan 2152*, WS | 31-1407 | Albert et al., 1992b (Morgan & Soltis) | L01899 | 8A, B |
| *Dudleya viscida* (S. Watson) Moran | Crassulaceae | Huntington BG 62801 | 31-1407 | Morgan & Soltis, 1993 | L11182 | 8A, B |
| *Kalanchöe daigremontana* Hamet & Perrier | Crassulaceae | *Morgan 2151*, WS | 31-1407 | Morgan & Soltis, 1993 | L11189 | 8A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Sedum rubrotinctum* Clausen | Crassulaceae | *Morgan 2153*, WS | 31-1407 | Albert et al., 1992b (Morgan & Soltis) | L01956 | 8A, B |
| *Crossosoma californicum* Nutt. | Crossosomataceae | Rancho Santa Ana BG | 31-1407 | Morgan & Soltis, 1993 | L11179 | 10A, B |
| *Cucumis sativus* L. | Cucurbitaceae | none | 27-1428 | Chase et al., 1993 (Swensen) | | 11B |
| *Cucurbita pepo* L. | Cucurbitaceae | none | 27-1428 | Chase et al., 1993 (Swensen) | | 11B, 16 |
| *Luffa quinquefida* (Hook. & Arn.) Seeman | Cucurbitaceae | *Heiser s.n.*, TENN | 27-1428 | Chase et al., 1993 (Swensen) | | 11B, 16 |
| *Bauera rubioides* Andrews | Cunoniaceae | Strybing Arb. 820237 | 31-1407 | Morgan & Soltis, 1993 | L11174 | 11A, C |
| *Ceratopetalum gummiferum* Small | Cunoniaceae | *Keller 2135*, CAS | 31-1407 | Albert et al., 1992b (Morgan & Soltis) | L01895 | 11A, C |
| *Callitris rhomboidea* R. Br. ex Rich. | Cupressaceae | *UNSW21734*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12537 | 3A, B |
| *Calocedrus decurrens* (Torr.) Florin | Cupressaceae | *UNSW22326*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12569 | |
| *Chamaecyparis obtusa* (Siebold & Zucc.) Endl. | Cupressaceae | *UNSW21735*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12570 | |
| *Cupressus sempervirens* L. | Cupressaceae | *UNSW14297*, UNSW | 57-1428 | Gadek & Quinn, 1993 | L12571 | |
| *Diselma archeri* Hook f. | Cupressaceae | *UNSW21742*, UNSW | 48-1428 | Gadek & Quinn, 1993 | L12572 | |
| *Juniperus conferta* Parl. | Cupressaceae | *UNSW14290*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12573 | |
| *Libocedrus plumosa* (D. Don) Sarg. | Cupressaceae | *UNSW21741*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12574 | |
| *Microbiota decussata* Komar. | Cupressaceae | *Gadek s.n.*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12575 | |
| *Platycladus orientalis* (L.) Franco | Cupressaceae | *UNSW21733*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L13172 | |
| *Tetraclinis articulata* (Vahl) Mast. | Cupressaceae | *UNSW21730*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12576 | |
| *Thuja occidentalis* L. | Cupressaceae | *UNSW21732*, UNSW | 57-1428 | Gadek & Quinn, 1993 | L12578 | |
| *Thujopsis dolobrata* (L. f.) Seibold & Zucc. | Cupressaceae | *UNSW21736*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12577 | |
| *Widdringtonia cedarbergensis* Marsh | Cupressaceae | *UNSW17574*, UNSW | 19-1428 | Gadek & Quinn, 1993 | L12538 | 3A, B |
| *Cyanastrum cordifolium* Oliv. | Cyanstraceae | *243187*, TRT | 41-1189 | Chase et al., 1993 (Graham & Barrett) | | 5A, B |
| *Cycas circinalis* L. | Cycadaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | L12674 | 3A, B |
| *Sphaeradenia pendula* Hammel | Cyclanthaceae | *M. W. Chase 222*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Carex hostiana* DC. | Cyperaceae | *Hedrén BL13*, UPS | 29-1428 | Chase et al., 1993 (Hedrén) | L12672 | 6A, B |
| *Cyperus alternifolius* L. | Cyperaceae | *Duvall 1992002*, UCR | 1-1352 | Duvall et al., 1993 (Duvall) | M91627 | 6A, B |
| *Cyrilla racemiflora* L. | Cyrillaceae | *Kron s.n.*, NCU | 29-1428 | Albert et al., 1992b (Kron) | L01900 | 13A, B |
| *Daphniphyllum* sp. | Daphniphyllaceae | *Qiu 91026*, NCU | 29-1428 | Albert et al., 1992b (Qiu) | L01901 | 8A, B, 16 |
| *Lomandra longifolia* Labill. | Dasypogonaceae | *Duvall 19920902*, UCR | 29-1355 | Duvall et al., 1993 (Duvall) | L05039 | 5B |
| *Datisca cannabina* L. | Datiscaceae | *Swensen s.n.*, RSA | 27-1428 | Chase et al., 1993 (Swensen) | | 11B |
| *Datisca glomerata* (C. Presl) Baill. | Datiscaceae | *Swensen s.n.*, TENN | 27-1428 | Chase et al., 1993 (Swensen) | | 11A, B, 16 |
| *Octomeles sumatrana* Miq. | Datiscaceae | *Philbrick 2273*, RSA | 27-1428 | Chase et al., 1993 (Swensen) | | 11A, B |
| *Tetrameles nudiflora* R. Br. | Datiscaceae | *Philbrick 2272*, RSA | 27-1428 | Chase et al., 1993 (Swensen) | | 11B, 16 |
| *Degeneria* sp. | Degeneriaceae | *J. M. Miller 1189-63*, ? | 29-1428 | Qiu et al., 1993 | L12643 | 4A, B |
| *Diapensia lapponica* L. | Diapensiaceae | *Hills 89018*, NCU | 29-1428 | Kron & Chase, 1993 | L12612 | 13A, B |
| *Alluaudia procera* Drake | Didieraceae | none | 1-1407 | Rettig et al., 1992 | M62563 | 9A, B |
| *Dillenia indica* L. | Dilleniaceae | *M. W. Chase 234*, NCU | 31-1428 | Albert et al., 1992b (Kron) | L01903 | 9A, 12B |
| *Dioscorea polygonoides* Humb. & Bonpl. | Dioscoreaceae | *M. W. Chase 197*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Dipsacus sativus* (L.) Honck. | Dipsacaceae | *Jansen 931*, MICH | 1-1428 | Olmstead et al., 1992 (Michaels) | L13824 | 14A, B |
| *Shorea stipularis* Thwaites | Dipterocarpaceae | *Dayanandan D2*, GF | 26-1428 | Chase et al., 1993 (Dyanandan) | | 10B |
| *Shorea zeylanica* (Thwaites) Ashton | Dipterocarpaceae | *Dayanandan D6*, GF | 26-1428 | Chase et al., 1993 (Dyanandan) | | 10B |
| *Sansevieria cylindrica* Bojer | Dracaenaceae | unknown | 1-1345 | Chase et al., 1993 (Eguiarte) | | 5A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Dionaea muscipula* Ellis | Droseraceae | none | 28-1428 | Albert et al., 1992b (Williams) | L01904 | 9B |
| *Drosera filiformis* Raf. | Droseraceae | *Albert 89Mi3*, NCU | 28-1428 | Albert et al., 1992b (Chase) | L01911 | 9A, B |
| *Drosera petiolaris* R. Br. | Droseraceae | none | 28-1351 | Albert et al., 1992b (Williams) | L01913 | 9B |
| *Drosera spathulata* Labill. | Droseraceae | none | 28-1428 | Chase et al., 1993 (Williams) | L13168 | 9B |
| *Diospyros virginiana* L. | Ebenaceae | *Kron 3004*, NCU | 29-1428 | Kron & Chase, 1993 | L12613 | 13A, B |
| *Ceratiola ericoides* Michx. | Empetraceae | *Kron 2069*, NCU | 29-1428 | Kron & Chase, 1993 | L12605 | 13A, B |
| *Dracophyllum longifolium* R. Br. | Epacridaceae | RBG Edinburgh 761673 | 29-1428 | Kron & Chase, 1993 | L12614 | 13A |
| *Cyathodes colensoi* Hook. | Epacridaceae | RBG Edinburgh 694055 | 29-1428 | Kron & Chase, 1993 | L12610 | 13A |
| *Epacris impressa* Labill. | Epacridaceae | RBG Edinburgh 680556 | 29-1428 | Albert et al., 1992b (Kron) | L01915 | 13A, B |
| *Leucopogon fraseri* A. Cunn. | Epacridaceae | RBG Edinburgh 341059 | 29-1428 | Kron & Chase, 1993 | L12620 | 13A |
| *Pentachondra pumila* (J. R. & G. Forst.) R. Br. | Epacridaceae | RBG Edinburgh 681038 | 29-1428 | Kron & Chase, 1993 | L12621 | 13A, B |
| *Ephedra tweediana* C. A. Mey. | Ephedraceae | none | 30-1428 | Chase et al., 1993 (Chase) | L12677 | 3A, B |
| *Arbutus canariensis* Duhamel | Ericaceae | RBG Edinburgh 752562 | 29-1428 | Kron & Chase, 1993 | L12597 | 13A, B |
| *Arctostaphylos uva-ursi* (L.) Spreng. | Ericaceae | Arnold Arb. 361-68 | 29-1428 | Kron & Chase, 1993 | L12598 | 13A |
| *Befaria racemosa* Vent. | Ericaceae | *Kron 2070*, NCU | 29-1428 | Kron & Chase, 1993 | L12600 | 13A, B |
| *Calluna vulgaris* (L.) Hull | Ericaceae | RBG Edinburgh 721433 | 29-988, 1170-1428 | Kron & Chase, 1993 | L12601 | 13A |
| *Cassiope mertensiana* (Bong.) G. Don | Ericaceae | Arnold Arb. 75-83 | 29-1428 | Kron & Chase, 1993 | L12603 | 13A, B |
| *Chamaedaphne calyculata* (L.) Moench | Ericaceae | RBG Edinburgh 752181 | 29-1428 | Kron & Chase, 1993 | L12606 | 13A, B |
| *Daboecia cantabrica* (Hudson) K. Koch | Ericaceae | RBG Edinburgh 751770 | 29-1428 | Kron & Chase, 1993 | L12611 | 13A, B |
| *Elliotia racemosa* Muhl. ex Elliot | Ericaceae | RBG Edinburgh 672632 | 29-1428 | Kron & Chase, 1993 | L12615 | 13A |
| *Enkianthus campanulatus* G. Nicholson | Ericaceae | Arnold Arb. 14528-C | 29-1428 | Kron & Chase, 1993 | L12616 | 13A, B |
| *Erica australis* L. | Ericaceae | RBG Edinburgh 781912 | 29-1428 | Kron & Chase, 1993 | L12617 | 13A, B |
| *Gaultheria eriophylla* (Pers.) Sleumer | Ericaceae | RBG Edinburgh 763043 | 29-641, 761-1428 | Kron & Chase, 1993 | L12618 | 13A, B |
| *Leiophyllum buxifolium* (Berg) Elliott | Ericaceae | *Kron 2067*, NCU | 29-1428 | Kron & Chase, 1993 | L12619 | 13A |
| *Leucothoë racemosa* (L.) Gray | Ericaceae | *Kron s.n.*, NCU | 29-1428 | Kron & Chase, 1993 | | 13A |
| *Rhododendron hippophaeoides* Balfour F. & Forrest | Ericaceae | RBG Edinburgh 321022 | 29-1428 | Olmstead et al., 1992 (Kron) | L01949 | 13A, B, 16 |
| *Vaccinium macrocarpon* Aiton | Ericaceae | *Hills 89019* NCU | 29-1428 | Kron & Chase, 1993 | L12625 | 13A, B |
| *Zenobia pulverulenta* (Bartram) Pollard | Ericaceae | Arnold Arb. 21087 | 29-1428 | Kron & Chase, 1993 | L12626 | 13A |
| *Lachnocaulon anceps* Morong | Eriocaulaceae | *M. W. Chase 211*, NCU | 27-1352 | Chase et al., 1993 (Chase) | | 6B |
| *Erythroxylum confusum* Britton | Erythroxylaceae | *Fairchild Trop. G 63-251E* | 31-1428 | Chase et al., 1993 (Chase) | L13183 | 11A, B |
| *Eucommia ulmoides* Oliv. | Eucommiaceae | *Qiu 91024*, NCU | 31-1428 | Albert et al., 1992b (Qiu) | L01917 | 15A, B, 16 |
| *Eucryphia lucida* Druce | Eucryphiaceae | Strybing Arb. 86-0250 | 31-1407 | Albert et al., 1992b (Morgan & Soltis) | L01918 | 11A, C |
| *Drypetes roxburghii* (Wall.) Hurus. | Euphorbiaceae | Lyon Arb., Hawaii | 27-1428 | Rodman et al., 1993 | M95757 | 11A, B |
| *Euphorbia polychroma* A. Kerner | Euphorbiaceae | *M. W. Chase 102*, NCU | 27-1428 | Chase et al., 1993 (Chase) | L13183 | 11A, B |
| *Eupomatia bennettii* F. Muell. | Eupomatiaceae | *Qiu 90022*, NCU | 29-1428 | Qiu et al., 1993 | L12644 | 4A, B |
| *Euptelea polyandra* Siebold & Zucc. | Eupteleaceae | *Qiu 90026*, NCU | 29-1428 | Chase et al., 1993 | L12645 | 7A, B, 16 |
| *Albizzia julibrisinii* Durazz. | Fabaceae | none | 511-1119 | Chase et al., 1993 (Learn & Clegg) | | 11A, B |
| *Bauhinia* sp. | Fabaceae | none | 293-413, 445-1339 | Chase et al., 1993 (Learn & Clegg) | | 11A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Medicago sativa* L. | Fabaceae | unknown | 1-1428 | Aldrich et al., 1986b | | 11A, B, 16 |
| *Pisum sativum* L. | Fabaceae | unknown | 1-1428 | Zurawski et al., 1986 | | 11A, B, 16 |
| *Chrysolepis (Castanopsis) sempervirens* (Kellogg) Hjelmq. | Fagaceae | *Qiu P90007*, NCU | 29-1428 | Chase et al., 1993 (Qiu) | | 11A, B, 16 |
| *Fagus americanus* Sweet | Fagaceae | unknown | 1-1307 | Chase et al., 1993 (Golenberg) | L13338 | 11A, B, 16 |
| *Nothofagus balansae* (Baill.) Steenis | Fagaceae | *J. Read s.n.*, Monash U, Victoria | 1-1400 | Chase et al., 1993 (Martin & Dowd) | L13344 | 11B, 16 |
| *Nothofagus dombeya* (Mirb.) Oerst. | Fagaceae | unknown | 27-1428 | Chase et al., 1993 (Golenberg) | L13350 | 11B, 16 |
| *Trigonobalanus verticellata* Forman | Fagaceae | RBG Edinburgh 1967-421 | 20-1428 | Chase et al., 1993 (Golenberg) | | 11B, 16 |
| *Flagellaria indica* L. | Flagellariaceae | *M. W. Chase 206*, NCU | 29-1428 | Chase et al., 1993 (Hedrén) | L12678 | 6A, B |
| *Fouquieria splendens* Engelm. | Fouquieriaceae | Matthaei BG 860162 (U Michigan) | 103-1428 | Olmstead et al., 1992 | L11675 | 13A, B |
| *Dicentra spectabilis* (L.) Lem. | Fumariaceae | *Les s.n.*, CONN | 29-1183 | Chase et al., 1993 (Les) | L08761 | 7A, B |
| *Garrya elliptica* Douglas ex Lindl. | Garryaceae | Rancho Santa Ana BG 13280 | 31-1407 | Albert et al., 1992b (Morgan & Soltis) | L01919 | 15A, B, 16 |
| *Exacum affine* Balf. f. ex Regel | Gentianaceae | none | 103-1428 | Olmstead et al., 1992 | L11684 | 15A, B |
| *Gentiana procera* Holm | Gentianaceae | none | 103-1428 | Olmstead et al., 1993 | L14398 | 15A, B |
| *Erodium texanum* A. Gray | Geraniaceae | *Van Devender s.n.*, ? | 26-1428 | Price & Palmer, 1993 | L14693 | |
| *Erodium ×variable* | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14694 | |
| *Geranium cinereum* Cav. | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14695 | |
| *Geranium grandiflorum* Gilib. | Geraniaceae | *Price s.n.*, IND | 26-1428 | Albert et al., 1992 (Price & Palmer) | L01920 | 10A, B |
| *Geranium macrorrhizum* L. | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14696 | |
| *Geranium madrense* Rose | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14697 | |
| *Geranium ocellatum* Cambess. | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14698 | |
| *Monsonia emarginata* (L.) L'Hérit. | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14701 | 10A, B |
| *Pelargonium capitatum* (L.) L'Hérit. | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14702 | |
| *Pelargonium cotyledonis* L'Hérit. | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14703 | |
| *Pelargonium existipulatum* L'Hérit. | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14704 | |
| *Pelargonium ×hortorum* | Geraniaceae | *Price s.n.*, IND | 26-1428 | Albert et al., 1992b (Price & Palmer) | L01941 | 10A, B |
| *Sarcocaulon vanderietiae* L. Bolus | Geraniaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14705 | |
| *Viviania marifolia* Cav. | Geraniaceae | *Penalillo 91000*, IND | 26-1428 | Price & Palmer, 1993 | L14707 | 10A, 11C |
| *Wendtia gracilis* Meyen | Geraniaceae | *Penalillo 91003*, IND | 26-1428 | Price & Palmer, 1993 | L14708 | 11C |
| *Streptocarpus holstii* Engl. | Gesneriaceae | Matthaei BG 85003 (U Michigan) | 103-1428 | Olmstead et al., 1993 | L14409 | 15A, B |
| *Ginkgo biloba* L. | Ginkgoaceae | *Price s.n.*, IND | 26-1351 | Chase et al., 1993 (Price) | | 1–3B |
| *Gnetum gemon* L. | Gnetaceae | *M. W. Chase 208*, NCU | 26-1351 | Chase et al., 1993 (Chase) | L12680 | 3A, B |
| *Scaevola frutescens* Krause | Goodeniaceae | Missouri BG 19426 | 1-1428 | Michaels et al., 1993 | L13932 | 14A, B |
| *Greyia radlkoferi* Szyszył. | Greyiaceae | Strybing Arb. 640406 | 31-1407 | Morgan & Soltis, 1993 | L11185 | 10A, 11C |
| *Brexia madagascarensis* Thouars ex Ger Gawl. | Grossulariaceae | *Soltis & Soltis s.n.*, WS | 31-1407 | Soltis et al., 1990 | L11176 | 11A, B |
| *Escallonia coquimbensis* Remy | Grossulariaceae | U. Calif. BG 52.1333 | 31-1407 | Morgan & Soltis, 1993 | L11183 | 14A, B |
| *Itea virginica* L. | Grossulariaceae | *D. M. E. Ware 9401*, WS | 31-1407 | Soltis et al., 1990 | L11188 | 8A, B |
| *Montinia caryophyllacea* Thunb. | Grossulariaceae | *Williams 2833*, MO | 31-1407 | Morgan & Soltis, 1993 | L11194 | 15A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Phyllonoma laticuspis* (Turcz.) Engl. | Grossulariaceae | *Morgan 2124*, WS | 31-1407 | Morgan & Soltis, 1993 | L11201 | 14A, B |
| *Pterostemon rotundifolius* Ramírez | Grossulariaceae | *Sanchez 259*, TEX | 31-1407 | Morgan & Soltis, 1993 | L11205 | 8B |
| *Ribes aureum* Pursh | Grossulariaceae | *Soltis & Soltis 2220*, WS | 31-1407 | Morgan & Soltis, 1993 | L11204 | 8A, B, 16 |
| *Tetracarpaea tasmanica* Hook. f. | Grossulariaceae | *Jordan s.n.*, HO | 31-1407 | Morgan & Soltis, 1993 | L11207 | 8A, B |
| *Gunnera manicata* Linden | Gunneraceae | *Kruckeberg s.n.*, WTU | 31-1407 | Morgan & Soltis, 1993 | L11186 | 7B, 12A, 16 |
| *Anigozanthos flavidus* DC. | Haemodoraceae | *M. W. Chase 159*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 6A, B |
| *Myriophyllum exalbescens* Fernald | Haloragaceae | *Broch* 30 Aug 1991, WS | 31-1407 | Morgan & Soltis, 1993 | L11195 | 8A, B |
| *Altingia* sp. | Hamamelidaceae | RBG, Edinburgh | 29-1428 | Chase et al., 1993 (Qiu) | | 8B, 16 |
| *Hamamelis mollis* Oliv. | Hamamelidaceae | *Qiu 91035*, NCU | 27-1428 | Albert et al. 1992b (Qiu) | L01922 | 8A, B, 16 |
| *Liquidambar formosana* Hance | Hamamelidaceae | *Qiu P92003*, NCU | 27-1428 | Chase et al., 1993 (Qiu) | | 16 |
| *Liquidambar orientalis* Miller | Hamamelidaceae | *Qiu P92001*, NCU | 27-1428 | Chase et al., 1993 (Qiu) | | 8B, 16 |
| *Rhodoleia championii* Hook. f. | Hamamelidaceae | RBG, Edinburgh | 27-1428 | Chase et al., 1993 (Qiu) | | 8A, B, 16 |
| *Heliconia latispatha* Benth. | Heliconiaceae | *Marie Selby BG 80-1610*, SEL | 31-1374 | Smith et al., 1993 | L05451 | 6A, B |
| *Heliconia puka* A. C. Sm. | Heliconiaceae | *Kress 79-1072*, SEL | 31-1374 | Smith et al., 1993 | L05452 | |
| *Hemerocallis fulva* L. | Hemerocallidaceae | *Duvall 19920601*, UCR | 32-1355 | Duvall et al., 1993 (Duvall) | L05036 | 5B |
| *Gyrocarpus* sp. | Hernandiaceae | *M. W. Chase 317*, NCU | 27-1428 | Qiu et al., 1993 | L12647 | 4B |
| *Hernandia ovigera* L. | Hernandiaceae | *J. Henrickson 3968*, NCU | 29-1428 | Qiu et al., 1993 | L12650 | 4A, B |
| *Galbulimima belgraveana* (F. Muell.) Sprague | Himatandraceae | *P. H. Weston 929*, NSW | 29-1428 | Qiu et al., 1993 | L12646 | 4A, B |
| *Humiria balsamifera* Aubl. | Humiriaceae | *W.R. Anderson 13701*, MICH | 31-1428 | Albert et al., 1992b (Chase) | L01926 | 11A, B |
| *Bowiea volubilis* Harv. ex Hook. f. | Hyacinthaceae | *M. W. Chase 176*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Ledebouria* (*Scilla*) *socialis* (Baker) Jessop | Hyacinthaceae | none | 29-1277 | Duvall et al., 1993 (Duvall) | L05038 | 5B |
| *Carpenteria californica* Torr. | Hydrangeaceae | *Soltis & Soltis 2478*, WS | 31-1407 | Soltis et al., 1990 | L11177 | 12A, B |
| *Decumaria* sp. | Hydrangeaceae | *Kron s.n.*, NCU | 29-1428 | Chase et al., 1993 (Kron) | | 12A, B |
| *Deutzia gracilis* Siebold & Zucc. | Hydrangeaceae | *Hufford s.n.*, DUL | 31-1407 | Morgan & Soltis, 1993 | L11181 | 12A, B |
| *Hydrangea macrophylla* Torr. | Hydrangeaceae | *Morgan 2150*, WS | 31-1407 | Morgan & Soltis, 1993 | L11187 | 12A, B, 16 |
| *Philadelphus lewisii* Pursh | Hydrangeaceae | *Soltis & Soltis 2411*, WS | 31-1407 | Morgan & Soltis, 1993 | L11198 | 12A, B, 16 |
| *Eriodictyon californicum* (Hook. & Arn) Torr. | Hydrophyllaceae | none | 27-1428 | Albert et al., 1992b (Olmstead) | L01916 | 15A, B |
| *Hydrolea ovata* Nutt. ex Choisy | Hydrophyllaceae | *Olmstead 89-009*, COLO | 27-1428 | Chase et al., 1993 (Olmstead) | L14293 | 15A |
| *Hydrophyllum virginianum* L. | Hydrophyllaceae | none | 27-1428 | Olmstead et al., 1992 | L01927 | 15A, B |
| *Curculigo capitata* Kuntze | Hypoxidaceae | *M. W. Chase 205*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Hypoxis leptocarpa* Engelm. | Hypoxidaceae | *M. W. Chase 108*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Idiospermum australiense* (Diels) S. T. Blake | Idiospermaceae | *Qiu 91042*, NCU | 29-1428 | Qiu et al., 1993 | L12651 | 4A, B |
| *Illicium parviflorum* Michx. ex Vent. | Illiciaceae | *Qiu 83*, NCU | 29-1428 | Qiu et al., 1993 | L12652 | 4A, B |
| *Anomatheca laxa* (Thunb.) Goldblatt | Iridaceae | *M. W. Chase 146*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Iris* ×*germanicum* L. | Iridaceae | *Bradley 25976*, GMUF | 32-1363 | Duvall et al., 1993 (Duvall) | L05037 | 5A, B |
| *Joinvillea plicata* Hook. f. | Joinvilleaceae | *Thien 84*, NO | 32-1351 | Duvall et al., 1993 (Duvall) | L01471 | |
| *Carya glabra* (Miller) Sweet | Juglandaceae | *M. W. Chase 254*, NCU | 27-1428 | Chase et al., 1993 (Qiu) | L12637 | 11B, 16 |
| *Juncus effusus* L. | Juncaceae | *M. W. Chase 200*, NCU | 29-1428 | Chase et al., 1993 (Chase) | L12681 | 6A, B |
| *Oxychloë andina* Phil. | Juncaceae | *Brooks s.n.*, KANU | 31-1407 | Chase et al., 1993 (Plunkett & Soltis) | L11168 | 6A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Prionium serratum* J. F. Drege | Juncaceae | *Brooks s.n.*, KANU | 31-1407 | Chase et al., 1993 (Plunkett & Soltis) | L11169 | 6A, B |
| *Koeberlinia spinosa* Zucc. | Koeberliniaceae | *Al-Shehbaz s.n.*, WIS | 27-1428 | Rodman et al., 1993 | L14600 | 10B |
| *Krameria lanceolata* Torr. | Krameriaceae | *Simpson 88-05-1-1*, MICH | 31-1428 | Chase et al., 1993 (Chase) | | 11A, B |
| *Lactoris fernandeziana* Phil. | Lactoridaceae | *Steussy 11335*, OS | 29-1183 | Chase et al., 1993 (Les) | L08763 | 4B |
| *Glechoma hederacea* L. | Lamiaceae | none | 27-1428 | Chase et al., 1993 (Olmstead) | L14292 | 15A |
| *Lamium purpureum* L. | Lamiaceae | *Wagstaff s.n.*, COLO | 27-1428 | Olmstead et al., 1993 | | 15B |
| *Physostegia virginiana* (L.) Benth. | Lamiaceae | *Olmstead 88-014*, COLO | 103-1428 | Olmstead et al., 1993 | L14405 | 15A, B |
| *Pogostemon patchouly* Pellet. | Lamiaceae | *Olmstead 89-008* COLO | 103-1428 | Olmstead et al., 1993 | L14406 | 15A, B |
| *Prostanthera rotundifolia* R. Br. | Lamiaceae | none | 103-1428 | Olmstead et al., 1993 | L14408 | 15A, B |
| *Salvia divinorum* Epling & Fátiva | Lamiaceae | Matthaei BG 850022 (U Michigan) | 27-1428 | Olmstead et al., 1993 | L14407 | 15A, B |
| *Scutellaria bolanderi* A. Gray | Lamiaceae | *Olmstead 395*, WTU | 27-1428 | Albert et al., 1992b (Olmstead) | L01954 | 15A, B |
| *Teucrium fruticans* L. | Lamiaceae | *Cantino 1287*, BHO | 103-1428 | Olmstead et al., 1993 | L14411 | 15A, B |
| *Akebia quinata* Decne. | Lardizabalaceae | *Qiu 91020*, NCU | 29-1428 | Chase et al., 1993 (Qiu) | L12627 | 7A, B, 16 |
| *Cinnamomum camphora* (L.) T. Nees & Eberm. | Lauraceae | *Qiu 102*, NCU | 29-1428 | Qiu et al., 1993 | L12641 | 4A, B |
| *Persea americana* Mill. | Lauraceae | unknown | 1-1428 | Golenberg et al., 1990 | | 4A, B |
| *Leitneria floridana* Chapm. | Leitneriaceae | *Qiu 91033*, NCU | 29-1428 | Chase et al., 1993 (Qiu) | | 10A, B, 16 |
| *Pinguicula caerulea* Walter | Lentibularicaeae | none | 27-1428 | Albert et al., 1992b (Chase) | L01942 | 15A, B |
| *Utricularia biflora* Roxb. | Lentibularicaeae | none | 27-1200 | Albert et al., 1992b (Chase) | L13190 | 15A, B |
| *Lilium superbum* L. | Liliaceae | *M. W. Chase 112*, NCU | 31-1428 | Olmstead et al., 1992 (Chase) | L12682 | 5A, B |
| *Medeola virginiana* (L.) Merr. | Liliaceae | *Bradley 24972*, GMUF | 32-1350 | Duvall et al., 1993 (Duvall) | M91613 | 5A, B |
| *Floerkea proserpinicoides* Willd. | Limnanthaceae | *Reznicek 8609*, MICH | 31-1428 | Chase et al., 1993 (Chase) | L12679 | 10A, B |
| *Limnanthes douglasii* R. Br. | Limnanthaceae | *Price s.n.*, IND | 26-1428 | Rodman et al., 1993 | L14700 | 10A, B |
| *Reinwardtia indica* Dumort. | Linaceae | *M. W. Chase 230*, NCU | 27-1366 | Chase et al., 1993 (Chase) | L13188 | 11B |
| *Anthocleista grandiflora* Gilg | Loganiaceae | *B. Bremer 2703*, UPS | 27-1443 | Olmstead et al., 1993 | L14389 | |
| *Fagraea* sp. | Loganiaceae | RBG, Kew 73: 12454 | 27-1443 | Olmstead et al., 1993 | L14396 | |
| *Gelsemium sempervivens* (L.) Pers. | Loganiaceae | Longwood BG 860395 | 103-341, 347-1428 | Olmstead et al., 1993 | L14397 | 15A, B |
| *Mostuea brunonis* Didr. | Loganiaceae | *M. Thulin 7831*, UPS | 27-1440 | Olmstead et al., 1993 | L14404 | |
| *Spigelia marilandica* L. | Loganiaceae | none | 27-1274 | Donoghue et al., 1992 (Olmstead) | L14007 | 15A, B |
| *Strychnos nux-vomica* L. | Loganiaceae | RBG, Kew 73: 12408 | 27-1440 | Olmstead et al., 1993 | L14410 | |
| *Orchidantha fimbriata* Holttum | Lowiaceae | *Kress & Beach 87-2159*, US | 31-1374 | Smith et al., 1993 | L05456 | 6A, B |
| *Orchidantha siamensis* K. Larsen | Lowiaceae | *Kress 92-3468*, US | 31-1374 | Smith et al., 1993 | L05457 | |
| *Lythrum hyssopifolia* L. | Lythraceae | *Baldwin 500*, DAV | 27-1428 | Conti et al., 1993 | L10218 | 10A, 11C |
| *Liriodendron chinense* (Hemsl.) Sarg. | Magnoliaceae | *Qiu 28*, NCU | 27-1428 | Qiu et al., 1993 | L12654 | 4B |
| *Liriodendron tulipifera* L. | Magnoliaceae | unknown | 1-1428 | Golenberg et al., 1990 | | 4A, B |
| *Magnolia hypoleuca* Siebold & Zucc. | Magnoliaceae | *Qiu 24*, NCU | 29-1428 | Qiu et al., 1993 | L12655 | 4A, B |
| *Magnolia macrophylla* L. | Magnoliaceae | unknown | 1-1428 | Golenberg et al., 1990 | | 4A |
| *Magnolia salicifolia* (Siebold & Zucc.) Maxim. | Magnoliaceae | *Qiu 82*, NCU | 29-1428 | Qiu et al., 1993 | L12656 | 4A, B |
| *Magnolia tripetala* L. | Magnoliaceae | *Qiu 3*, NCU | 29-1428 | Qiu et al., 1993 | | 4A |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Mangletia fordiana* (Hemsl.) Oliv. | Magnoliaceae | *Qiu 26*, NCU | 29-1428 | Qiu et al., 1993 | L12658 | 4A, B |
| *Michelia figo* (Lour.) Spreng. | Magnoliaceae | *Qiu 27*, NCU | 29-1428 | Qiu et al., 1993 | L12659 | 4A, B |
| *Talauma ovata* A. St.-Hil. | Magnoliaceae | *W. R. Anderson 13623*, NCU | 29-1428 | Qiu et al., 1993 | L12666 | 4A, B |
| *Talauma singaporensis* Ridl. | Magnoliaceae | *Qiu 91038*, NCU | 29-1428 | Qiu et al., 1993 | L12667 | 4A |
| *Acridocarpus natalitius* A. Juss. | Malpighiaceae | *Goldblatt s.n.*, MO | 29-1428 | Chase et al., 1993 (Chase) | | 11A, B |
| *Bunchosia armeniaca* (Cav.) DC. | Malpighiaceae | *Fairchild Trop. G 77999*, MICH | 29-1428 | Chase et al., 1993 (Chase) | | 11A |
| *Byrsonima crassifolia* (L.) Kunth | Malpighiaceae | *Fairchild Trop. G 81680*, MICH | 29-1428 | Albert et al., 1992b (Chase) | L01892 | 11A, B, 16 |
| *Dicella nucifera* Chodat | Malpighiaceae | *W. R. Anderson 13607*, MICH | 31-1428 | Chase et al., 1993 (Chase) | | 11A, B, 16 |
| *Galphimia gracilis* Bartl. | Malpighiaceae | *Adelson s.n.*, MICH | 31-1428 | Chase et al., 1993 (Chase) | | 11A, B |
| *Mascagnia stannea* (Griseb.) Nied. | Malpighiaceae | *Plowman 5865*, MICH | 31-1428 | Chase et al., 1993 (Chase) | | 11A, B |
| *Thryallis latifolia* Mart. | Malpighiaceae | *W. R. Anderson 13657*, MICH | 29-1428 | Chase et al., 1993 (Chase) | | 11A, B |
| *Gossypium robinsonii* F. Muell. | Malvaceae | *Wendel s.n.*, ISC | 27-1428 | Chase et al., 1993 (Chase) | L13186 | 10A, B |
| *Thespesia populnea* (L.) Sol. ex Correa | Malvaceae | *Wendel s.n.*, ISC | 27-1428 | Albert et al., 1992b (Chase) | L01961 | 10B |
| *Calathea loeseneri* J. F. Macb. | Marantaceae | *Marie Selby BG 85-31*, SEL | 31-1374 | Smith et al., 1993 | L05444 | 6A, B |
| *Maranta leuconeura* E. Morris | Marantaceae | *Bradely 24979*, GMUF | 32-1351 | Duvall et al., 1993 (Duvall) | L05040 | 6A, B |
| *Marantochloa purpurea* (Ridl.) Milne-Redh. | Marantaceae | *Kress 78-894*, | 31-1374 | Smith et al., 1993 | L05453 | |
| *Aletris farinosa* L. | Melanthiaceae | *M. W. Chase 1105* NCU | 31-1428 | Chase et al., 1993 (Chase) | | |
| *Chamaelirium luteum* (L.) A. Gray | Melanthiaceae | *M. W. Chase 224*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Pleea tenuifolia* Michx. | Melanthiaceae | *M. W. Chase 152*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Veratrum parviflorum* Michx. | Melanthiaceae | *Chase s.n.*, NCU | 64-1428 | Chase et al., 1993 (Chase) | | 5B |
| *Mouriria cyphocarpa* Standl. | Melastomataceae | *Nepokroeff & Hammel 724*, WIS | 27-1428 | Chase et al., 1993 (Conti) | | 11C |
| *Osbeckia stellata* Wall. | Melastomataceae | *Conti 1004*, WIS | 27-1428 | Chase et al., 1993 (Conti) | | 11C |
| *Cissampelos* sp. | Menispermaceae | none | 27-319, 506-1261 | Qiu et al., 1993 | | |
| *Cocculus trilobus* (Thunb.) DC. | Menispermaceae | *Qiu 91016*, NCU | 29-1428 | Chase et al., 1993 (Qiu) | L12642 | 7A, B, 16 |
| *Menyanthes trifoliata* L. | Menyanthaceae | none | 103-1428 | Olmstead et al., 1993 | L14006 | 14A, B |
| *Villarsia calthifolia* F. Muell. | Menyanthaceae | *Ornduff 9726*, COLO | 103-1428 | Olmstead et al., 1992 | L11685 | 14A, B |
| *Mollugo verticellata* L. | Molluginaceae | *Rettig s.n.*, TAMU | 1-1407 | Rettig et al., 1992 | M62566 | 9A, B |
| *Hedycarya arborea* J. R. & G. Forst. | Monimiaceae | *Qiu 90028*, NCU | 29-1428 | Qiu et al., 1993 | L12648 | 4A, B |
| *Ficus trigonata* L. | Moraceae | unknown | 301-1203 | Chase et al., 1993 (Herre) | | 11B, 16 |
| *Morus alba* L. | Moraceae | none | 1-1203 | Albert et al., 1992b (Golenberg) | L01933 | 11A, B, 16 |
| *Moringa oleifera* Lam. | Moringaceae | *Iltis 30501*, WIS | 27-1428 | Rodman et al., 1993 | L11359 | 10A, B |
| *Ensete ventricosum* (Welw.) Cheesman | Musaceae | unknown | 31-1374 | Smith et al., 1993 | L05448 | |
| *Musa acuminata* Colla | Musaceae | unknown | 31-1374 | Smith et al., 1993 | L05455 | 6A, B |
| *Myrica cerifera* L. | Myricaceae | *Qiu 91036*, NCU | 29-1428 | Albert et al., 1992b (Qiu) | L01934 | 11A, B, 16 |
| *Knema latericia* Elmer | Myristacaceae | *Qiu 91041*, NCU | 29-1428 | Qiu et al., 1993 | L12653 | 4A, B |
| *Ardisia crenata* Sims | Myrsinaceae | *Kron 3001*, NCU | 29-1428 | Kron & Chase, 1993 | L12599 | 13A, B |
| *Heteropyxis natalensis* Harv. | Myrtaceae | *Conti 1002*, WIS | 27-1428 | Chase et al., 1993 (Conti) | | 11C |
| *Nelumbo lutea* (Willd.) Pers. | Nelumbonaceae | *Les s.n.*, CONN | 29-1183 | Les et al., 1991 | M77032 | 7A, B, 16 |
| | | *Qiu 91028*, NCU | 1184-1428 | Qiu et al., 1993 | | |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Nelsonia canescens* (Lam.) Nees | Nelsoniaceae | *RBG, Kew, 25356-25301*, UPS | 29-1428 | Albert et al., 1992b (Hedrén) | L01935 | 15A |
| *Nepenthes alata* Blanco | Nepenthaceae | *M. W. Chase 145*, NCU | 31-1428 | Albert et al., 1992b (Chase) | L01936 | 9A, B |
| *Nolina lindheimerina* (Scheele) S. Watson | Nolinaceae | unknown | 32-1332 | Chase et al., 1993 (Eguiarte) | | 5A, B |
| *Nolina* (*Beaucarnea*) *recurvata* (Lem.) Hemsl. | Nolinaceae | *Peterson s.n.*, US | 32-1352 | Duvall et al., 1993 (Duvall) | L05030 | 5A |
| *Mirabilis jalapa* L. | Nyctaginaceae | *Rettig 1657*, TAMU | 1-1407 | Rettig et al., 1992 | M62565 | 9A, B |
| *Euryale ferox* Salisb. | Nymphaeaceae | *Les s.n.*, CONN | 29-1183 | Les et al., 1991 | M77031 | 4A, B |
| *Nuphar variegata* Durand | Nymphaeaceae | *Les s.n.*, CONN | 29-1183 | Les et al., 1991 | M77034 | 4A, B |
| *Nymphaea odorata* Aiton | Nymphaeaceae | *Les s.n.*, CONN | 29-1183 | Les et al., 1991 | M77035 | 4A, B |
| | | *Qiu 91029*, NCU | 1184-1428 | Qiu et al., 1993 | | |
| *Victoria cruziana* Orb. | Nymphaeaceae | *Les s.n.*, CONN | 29-1183 | Les et al., 1991 | M77036 | 4A, B |
| *Camptotheca acuminata* Decne. | Nyssaceae | Strybing Arb. 74-180 | 31-1407 | Albert et al., 1992b (Xiang) | L01937 | 12A, B |
| *Davidia involucrata* Baill. | Nyssaceae | U.S. Natl. Arb. 12067 | 31-1407 | Xiang et al., 1993 | L11223 | 12A, B |
| *Nyssa ogeche* Marsh | Nyssaceae | U.S. Natl. Arb. s.n. | 31-1407 | Xiang et al., 1993 | L11228 | 12A, B |
| *Ochna multiflora* DC. | Ochnaceae | *M. W. Chase 229*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 11A, B |
| *Schoepfia schreberi* J. F. Gmel. | Olacaceae | *Nickrent 2599*, ILL | 31-1407 | Morgan & Soltis, 1993 | L11205 | 9B, 12A |
| *Jasminum suavissimum* Lindl. | Oleaceae | Matthaei BG 850259 (U Michigan) | 27-1428 | Albert et al., 1992b (Olmstead) | L01929 | 15A, B |
| *Ligustrum vulgare* L. | Oleaceae | *Olmstead s.n.*, COLO | 103-1428 | Olmstead et al., 1992 | L11686 | 15A, B |
| *Circaea alpina* L. | Onagraceae | *Smith 1052*, WIS | 27-1428 | Conti et al., 1993 | L10216 | 10A, 11C |
| *Clarkia xantiana* A. Gray | Onagraceae | *Gottlieb 7436*, DAV | 10-1428 | Olmstead et al., 1992 (Conti) | L10896 | 10A, 11C |
| *Epilobium angustifolium* L. | Onagraceae | *Sytsma 5012*, WIS | 10-1407 | Conti et al., 1993 | L10217 | 10A, 11C |
| *Fuchsia cyrtandroides* J. W. Moore | Onagraceae | *Berry et al. 4618*, MO | 27-1428 | Conti et al., 1993 | L10220 | 10A |
| *Hauya elegans* DC. | Onagraceae | *Moreno 11352*, MO | 27-1428 | Conti et al., 1993 | L10227 | 10A, 11C |
| *Lopezia riesenbachia* Plitmann, Raven & Breedlove | Onagraceae | *Anderson & Anderson 5626*, MICH | 27-1428 | Conti et al., 1993 | L10219 | 10A, 11C |
| *Ludwigia peploides* (Kunth) Raven | Onagraceae | *Sytsma 5010*, WIS | 27-1428 | Conti et al., 1993 | L10222 | 10A, 11C |
| *Ludwigia peruviana* (L.) Hara | Onagraceae | *Zardini & Gentry 2206*, MO | 27-1428 | Conti et al., 1993 | L10221 | |
| *Oenothera elata* Kunth | Onagraceae | unknown | 1-1407 | Winter & Herrmann, 1988 | | 10, 11C |
| *Cypripedium irapeanum* Lex. in La Llave & Lex. | Orchidaceae | *Albert s.n.*, NCU | 49-1352 | Chase et al., 1993 (Albert) | | 5B |
| *Neuwiedia veratrifolia* Blume | Orchidaceae | *Clements 5910*, CANB | 31-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Oncidium excavatum* Lindl. | Orchidaceae | *M. W. Chase 83427*, K | 1-1428 | Olmstead et al., 1992 (Chase) | | 5A, B |
| *Averrhoa carambola* L. | Oxalidaceae | *Price s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14692 | 11C |
| *Hypseocharis* sp. | Oxalidaceae | *Beck s.n.*, IND | 26-1428 | Price & Palmer, 1993 | L14699 | 10B |
| *Oxalis dillenii* Jacq. | Oxalidaceae | *Price s.n.*, IND | 26-1428 | Albert et al., 1992b (Price & Palmer) | L01938 | 11A, C |
| *Paeonia tenuifolia* L. | Paeoniaceae | *Kron 2115*, NCU | 29-1428 | Chase et al., 1993 (Kron) | L13687 | 8B, 12A, 16 |
| *Freycinetia scandens* Gaudich | Pandanaceae | *M. W. Chase 191*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Pandanus veitchii* Mast. & Moore | Pandanaceae | *Duvall 19920301*, UCR | 32-1428 | Duvall et al., 1993 (Duvall) | M91632 | 5B |
| *Papaver orientale* L. | Papaveraceae | *Les s.n.*, CONN | 29-1183 | Chase et al., 1993 (Les) | L08764 | 7A, B, 16 |
| *Sanguinaria canadensis* L. | Papaveraceae | *Qiu 91032*, NCU | 29-1428 | Albert et al., 1992b (Qiu) | L01951 | 7A, B, 16 |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Passiflora quadrangularis* L. | Passifloraceae | *Kron 3000*, NCU | 26-1428 | Albert et al., 1992b (Kron) | L01940 | 11A, B |
| *Harpagophytum granidieri* Baill. | Pedaliaceae | *Morden 90.66*, IND | 29-1428 | Albert et al., 1992b (Hedrén) | L01923 | 15A, B |
| *Proboscidea lousianica* Thell. | Pedaliaceae | *Morden 857*, IND | 29-1428 | Albert et al., 1992b (Hedrén) | L01946 | 15A, B |
| *Sesamum indicum* L. | Pedaliaceae | none | 103-1274, 1294-1428 | Olmstead et al., 1993 | L14408 | 15A, B |
| *Philydrum lanuginosum* Banks & Gaertn. | Philydraceae | *243186*, TRT | 40-1190 | Chase et al., 1993 (Graham & Barrett) | | 6A, B |
| *Phytolacca americana* L. | Phytolaccaceae | *Rettig 1651*, TAMU | 1-1407 | Rettig et al., 1992 | M62567 | 9A, B |
| *Rivina humilis* L. | Phytolaccaceae | unknown | 1-1407 | Rettig et al., 1992 | M62569 | 9A, B |
| *Stegnosperma halimifolium* Benth. | Phytolaccaceae | none | 1-1407 | Rettig et al., 1992 | M62570 | 9A, B |
| *Abies magnifica* A. Murray | Pinaceae | Inst. Forest Genetics 30/32 | 1-1404 | Chase et al., 1993 (Strauss) | | 3A, B |
| *Cedrus deodora* (Roxb.) Loudon | Pinaceae | Inst. Forest Genetics 87/26 | 1-1428 | Chase et al., 1993 (Strauss) | X63662 | 3A, B |
| *Keteleeria davidiana* (Bertram) Beissn. | Pinaceae | UC Berkeley BG 35.1252 | 1-1428 | Chase et al., 1993 (Strauss) | X63664 | 3A, B |
| *Larix occidentalis* Nutt. | Pinaceae | none | 1-1428 | Chase et al., 1993 (Strauss) | X63663 | 3A, B |
| *Picea pungens* Engelm. | Pinaceae | none | 1-1428 | Chase et al., 1993 (Strauss) | X58136 | 3A, B |
| *Picea sitchensis* (Bong.) Carrière | Pinaceae | none | 1-1428 | Chase et al., 1993 (Strauss) | X63660 | 3A |
| *Pinus griffithii* McClell. | Pinaceae | Inst. Forest Genetics 36/32 | 1-1428 | Bousquet et al., 1992 | X58131 | 3A, B |
| *Pinus radiata* D. Don | Pinaceae | none | 1-1428 | Bousquet et al., 1992 | X58134 | 3A, B |
| *Pseudolarix amabilis* Rehder | Pinaceae | none | 1-1404 | Chase et al., 1993 (Strauss) | X58782 | 3A, B |
| *Pseudotsuga menziesii* (Mirb.) Franco | Pinaceae | unknown | 1-1428 | Hipkins et al., 1990 | X52937 | 3A, B |
| *Tsuga heterophylla* (Raf.) Sarg. | Pinaceae | none | 1-1428 | Chase et al., 1993 (Strauss) | X63659 | 3A, B |
| *Peperomia* sp. | Piperaceae | *Qiu 91047*, NCU | 27-1428 | Qiu et al., 1993 | L12661 | 4A, B |
| *Piper betle* L. | Piperaceae | *Qiu 91048*, NCU | 27-1428 | Qiu et al., 1993 | L12660 | 4B |
| *Pittosporum japonicum* Hort. ex C. Presl | Pittosporaceae | *Rieseberg s.n.*, RSA | 31-1407 | Morgan & Soltis, 1993 | L11202 | 14A, B |
| *Platanus occidentalis* L. | Platanaceae | *Qiu P90005*, NCU | 29-1428 | Albert et al., 1992b (Qiu) | L01943 | 7A, B, 16 |
| *Plumbago capensis* Thunb. | Plumbaginaceae | unknown | 1-1428 | Giannasi et al., 1992 | M77701 | 9A, B |
| *Aegilops crassa* Boiss. | Poaceae | unknown | 1-1428 | Terachi et al., 1987 | | 6A, B |
| *Avena sativa* L. | Poaceae | unknown | 1-1428 | Chase et al., 1993 (Garcia, U Leon) | | 6A, B |
| *Bambusa multiplex* (Lour.) Rausch | Poaceae | *Sanders 62-616*, UCR | 32-1355 | Duvall et al., 1993 (Duvall) | M91626 | 6B |
| *Cenchrus setigerus* Vahl | Poaceae | unknown | 1-1428 | Doebley et al., 1990 | | 6A, B |
| *Hordeum vulgare* L. | Poaceae | unknown | 1-1428 | Zurawski et al., 1984 | X00630 | 6A |
| *Neurachne tenuifolia* S. T. Blake | Poaceae | unknown | 1-1428 | Hudson et al., 1990 | | 6A, B |
| *Oryza sativa* L. | Poaceae | unknown | 1-1428 | Nishizawa & Hirai, 1987 | D00207 | 6A, B |
| *Pennisetum glaucum* (L.) R. Br. | Poaceae | unknown | 1-1428 | Doebley et al., 1990 | | 6A |
| *Pucinellia distans* (Jaq.) Parl. | Poaceae | unknown | 1-1428 | Doebley et al., 1990 | | 6A |
| *Triticum aestivum* L. | Poaceae | unknown | 1-1428 | Terachi et al., 1987 | | 6A, B |
| *Zizania taxana* Hitchc. | Poaceae | *Duvall s.n.*, MIN | 29-1351 | Duvall et al., 1993 (Duvall) | | |
| *Podocarpus gracilior* Pilg. | Podocarpaceae | UC Berkeley BG 28.175 | 1-1428 | Bousquet et al., 1992 | X58135 | 3A, B |
| *Polemonium reptans* L. | Polemoniaceae | none | 103-1428 | Olmstead et al., 1992 | L11687 | 13A, B |
| *Polygala cruciata* L. | Polygalaceae | *M. W. Chase 155*, NCU | 29-1428 | Albert et al., 1992b (Chase) | L01945 | 11A, B, 16 |
| *Securidaca diversifolia* (L.) S. F. Blake | Polygalaceae | *Adelson s.n.*, MICH | 30-1428 | Olmstead et al., 1992 (Chase) | L01955 | 11A, B |
| *Rheum* ×*cultorum* | Polygonaceae | unknown | 1-1428 | Giannasi et al., 1992 | M77702 | 9A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Pontederia sagittata* C. Presl | Pontederiaceae | unknown | 81-1155, 1182-1321 | Duvall et al., 1993 (Clark) | | 6A, B |
| *Portulaca grandiflora* Hook. | Portulacaceae | *Rettig 1656*, TAMU | 1-1407 | Rettig et al., 1992 | M62568 | 9A, B |
| *Potamogeton amplifolius* Tuck. | Potamogetonaceae | *Les 483*, CONN | 29-1183 | Chase et al., 1993 (Les) | L08765 | 5A, B |
| *Anagallis arvensis* L. | Primulaceae | *Rettig 1653*, TAMU | 1-1428 | Chase et al., 1993 (Rettig) | M88343 | 13A, B |
| *Lambertia inermis* R. Br. | Proteaceae | Natl. Trop. BG, Hawaii | 31-1407 | Morgan & Soltis, 1993 | L11190 | 7A, B, 16 |
| *Punica granatum* L. | Punicaceae | *Conti 1001*, WIS | 27-1428 | Conti et al., 1993 | L10223 | 11C |
| *Pyrola rotundifolia* L. | Pyrolaceae | *Kron 1906*, NCU | 29-1428 | Kron & Chase, 1993 | L12622 | 13A, B |
| *Caltha palustris* L. | Ranunculaceae | none | 27-1428 | Olmstead et al., 1993 | L02431 | 7A, B, 16 |
| *Ranunculus trichophyllus* Chaix | Ranunculaceae | *Les s.n.*, CONN | 29-1183 | Chase et al., 1993 (Les) | L08766 | 7A, B, 16 |
| *Xanthorhiza simplicissima* Marshall | Ranunculaceae | *Qiu 91030*, NCU | 29-1428 | Chase et al., 1993 (Qiu) | L12669 | 7A, B, 16 |
| *Stegolepis allenii* Steyerm. | Rapateaceae | unknown | 1-1428 | Duvall et al., 1993 (Clark) | | 6A, B |
| *Reseda alba* L. | Resedaceae | *Price s.n.*, IND | 27-1428 | Rodman et al., 1993 | M95756 | 10A, B |
| *Elegia* sp. | Restionaceae | *M. W. Chase 209*, NCU | 29-1428 | Duvall et al., 1993 (Hedrén) | L12675 | 6A, B |
| *Rhamnus cartharticus* L. | Rhamnaceae | *M. W. Chase 100*, NCU | 30-1428 | Chase et al., 1993 (Chase) | L13189 | 11A, B, 16 |
| *Geum chiloense* Balb. ex Ser. | Rosaceae | *Morgan 2137*, WS | 31-1407 | Albert et al., 1992b (Morgan & Soltis) | L01921 | 11A, B, 16 |
| *Photinia fraseri* Dress | Rosaceae | *Morgan 2131*, WS | 31-1407 | Morgan & Soltis, 1993 | L11200 | 11A, B |
| *Prunus virginiana* L. | Rosaceae | *Soltis & Soltis 2475*, WS | 31-1407 | Albert et al., 1992b (Morgan & Soltis) | L01947 | 11A, B, 16 |
| *Spiraea vanhouttei* (Briot) Zabel | Rosaceae | *Morgan 2130*, WS | 31-1407 | Morgan & Soltis, 1993 | L11206 | 11A, B, 16 |
| *Chiococca alba* (L.) A. Hitch. | Rubiaceae | *B. Bremer 3098*, UPS | 27-1437 | Olmstead et al., 1993 | L14394 | |
| *Pentas lanceolata* (Forssk.) Deflers | Rubiaceae | *Jansen 914*, MICH | 27-243, 249-1231, 1237-1428 | Michaels et al., 1993 | L13931 | 15A, B |
| *Danae racemosa* Moench | Ruscaceae | *M. W. Chase 121*, NCU | 29-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Danae racemosa* Moench | Ruscaceae | *Duvall 19920901*, UCR | 20-1351 | Duvall et al., 1993 (Duvall) | L05034 | |
| *Poncirus trifoliata* (L.) Raf. | Rutaceae | *M. W. Chase 117*, NCU | 30-1428 | Chase et al., 1993 (Chase) | | 10A, B |
| *Sabia* sp. | Sabiaceae | *Qiu 91025*, NCU | 29-1428 | Chase et al., 1993 (Qiu) | L12662 | 7A, B, 16 |
| *Osyris lanceolata* Hochst. & Steud. | Santalaceae | *Nickrent 2731*, SIU | 31-1407 | Morgan & Soltis, 1993 | L11196 | 9B, 12A |
| *Cupaniopsis anacardioides* Radlk. | Sapindaceae | *M. W. Chase 217*, NCU | 27-1428 | Chase et al., 1993 (Chase) | L13182 | 10A, B |
| *Chrysophyllum oliviforme* L. | Sapotaceae | *M. W. Chase 127*, NCU | 29-1428 | Kron & Chase, 1993 | L12607 | 13A, B |
| *Manilkara zapota* (L.) Royen | Sapotaceae | *M. W. Chase 129*, NCU | 29-1428 | Albert et al., 1992b (Chase) | L01932 | 13A, B |
| *Sargentodoxa cuneata* (Oliv.) Rehder & Wilson | Sargentodoxaceae | *Qiu 91043*, NCU | 29-1428 | Chase et al., 1993 (Qiu) | | 11B, 16 |
| *Heliamphora nutans* Benth. | Sarraceniaceae | none | 27-1351 | Albert et al., 1992b (Williams) | L02433 | 13B |
| *Sarracenia flava* L. | Sarraceniaceae | *M. W. Chase 144*, NCU | 29-1428 | Albert et al., 1992b (Kron) | L01952 | 13A, B |
| *Houttuynia cordata* Thunb. | Saururaceae | *Les s.n.*, CONN | 29-1183 | Chase et al., 1993 (Les) | L08762 | 4A, B |
| *Saururus cernuus* L. | Saururaceae | *Olmstead 88-006*, COLO | 27-1428 | Chase et al., 1993 (Olmstead) | L14294 | 4A, B |
| *Astilbe taquetii* (Lév.) Koidz. | Saxifragaceae | *Soltis & Soltis 2477*, WS | 31-1407 | Soltis et al., 1990 | L11173 | 8A |
| *Boykinia rotundifolia* Parry | Saxifragaceae | *Gornall 101*, UBC | 31-1407 | Morgan & Soltis, 1993 | L11175 | 8A, B |
| *Darmera peltata* (Torr.) Voss | Saxifragaceae | *Soltis & Soltis 2083*, WS | 31-1407 | Morgan & Soltis, 1993 | L11180 | |
| *Francoa sonchifolia* Cav. | Saxifragaceae | *Soltis & Soltis 2479*, WS | 31-1407 | Soltis et al., 1990 | L11184 | 10A, 11C |
| *Heuchera micrantha* Douglas | Saxifragaceae | *Soltis & Soltis 1949*, WS | 31-1407 | Soltis et al., 1990 | L01925 | 8A, B, 16 |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Leptarrhena pyrolifolia* (D. Don) R. Br. | Saxifragaceae | *Soltis & Soltis 2237*, WS | 31-1407 | Morgan & Soltis, 1993 | L11191 | |
| *Lepuropetalon spathulatum* (Muhl.) Elliott | Saxifragaceae | *Thomas s.n.*, NLU | 31-1407 | Morgan & Soltis, 1993 | L11192 | 11A, B |
| *Parnassia fimbriata* Banks | Saxifragaceae | *Soltis & Soltis s.n.*, WS | 31-1407 | Soltis et al., 1990 | L01939 | 11A, B |
| *Penthorum sedoides* L. | Saxifragaceae | *W. S. Hayden 2232*, WS | 31-1407 | Soltis et al., 1990 | L11197 | 8A, B |
| *Saxifraga integrifolia* Hook. | Saxifragaceae | *Soltis & Soltis 2253*, WS | 31-1407 | Morgan & Soltis, 1993 | L01953 | 8A, B, 16 |
| *Vahlia capensis* Thunb. | Saxifragaceae | *Van Wyk 10-579*, PRU | 31-1407 | Morgan & Soltis, 1993 | L11208 | 15B |
| *Schisandra sphenanthera* Rehder & Wilson | Schisandraceae | *Qiu 73*, NCU | 29-1428 | Qiu et al., 1993 | L12665 | 4A, B |
| *Antirrhinum majus* L. | Scrophulariaceae | *dePamphilis s.n.*, ? | 103-1428 | Olmstead et al., 1992 | L11688 | 15A, B |
| *Digitalis purpurea* L. | Scrophulariaceae | none | 27-1428 | Albert et al., 1992b (Olmstead) | L01902 | 15A, B |
| *Ailanthus altissima* L. | Simaroubaceae | *M. W. Chase 126*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 10A, B |
| *Smilax glauca* Walter | Smilacaceae | *M. W. Chase 107*, NCU | 30-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Lycopersicon esculentum* Mill. | Solanaceae | none | 103-1428 | Olmstead et al., 1993 | L14403 | 15A, B |
| *Nicotiana tabacum* L. | Solanaceae | unknown | 1-1428 | Lin et al., 1986 | | 15A, B, 16 |
| *Petunia hybrida* (Hook. f.) Vilm. | Solanaceae | unknown | 1-1404 | Aldrich et al., 1986a | | 15A, B |
| *Sparganium americanum* Nutt. | Sparganiaceae | *M. W. Chase 257*, NCU | 20-1351 | Duvall et al., 1993 (Duvall) | M91633 | 6B |
| *Theobroma cacao* L. | Sterculiaceae | *Alverson s.n.*, WIS | 27-1428 | Chase et al., 1993 (Karol) | | 10B |
| *Phenakospermum guyannense* (Rich.) Miq. | Strelitziaceae | *Kress 86-2099*, SEL | 31-1374 | Smith et al., 1993 | L05458 | 6A, B |
| *Ravenala madagascariensis* J. F. Gmel. | Strelitziaceae | *Kress 92-3504*, US | 31-1374 | Smith et al., 1993 | L05459 | |
| *Ravenala madagascariensis* J. F. Gmel. | Strelitziaceae | unknown | 1-71, 78-100, 161-264, 301-1053, 1077-1276, 1315-1369 | Duvall et al., 1993 (Clark) | | 6A, B |
| *Strelitzia nicolae* Regel & Koch | Strelitziaceae | *Kress 91-3169*, US | 31-1374 | Smith et al., 1993 | L05461 | 6A, B |
| *Styrax americana* Lam. | Styracaceae | *Kron 3002*, NCU | 29-1428 | Kron & Chase, 1993 | L12623 | 13A, B |
| *Symplocus paniculata* Miq. | Symplocaceae | *Kron 3005*, NCU | 29-1428 | Kron & Chase, 1993 | L12624 | 13A, B |
| *Tacca chantrieri* André | Taccaceae | *M. W. Chase 175*, NCU | 31-1428 | Chase et al., 1993 (Chase) | | 5A, B |
| *Taxus ×media* | Taxaceae | *Price s.n.*, IND | 27-1351 | Chase et al., 1993 (Price) | | 3B |
| *Athrotaxis selaginoides* D. Don | Taxodiaceae | UC Berkeley BG | 27-1351 | Chase et al., 1993 (Price) | | 3B |
| *Metasequoia glyptostroboides* Hu & W. C. Cheng | Taxodiaceae | none | 2-1365 | Chase et al., 1993 (Strauss) | | 3A, B |
| *Sciadopitys verticillata* (Thunb.) Siebold & Zucc. | Taxodiaceae | UC Berkeley BG | 27-1351 | Chase et al., 1993 (Price) | | 3B |
| *Sequoiadendron giganteum* (Lindl.) J. Buchholz | Taxodiaceae | none | 1-1428 | Chase et al., 1993 (Strauss) | | 3A, B |
| *Taxodium distichum* (L.) Rich. | Taxodiaceae | *Brunsfeld 3084*, IDF | 2-1365 | Soltis, Soltis & Smiley, 1992 | | 3A, B |
| *Tetracentron sinensis* Oliv. | Tetracentraceae | *Qiu 90009*, NCU | 27-1428 | Chase et al., 1993 (Qiu) | L12668 | 7A, B, 16 |
| *Camellia japonica* L. | Theaceae | none | 29-1428 | Kron & Chase, 1993 (Qiu) | L12602 | 13A, B |
| *Clavija eggersiana* Mez | Theophrastaceae | *M. W. Chase 216*, NCU | 29-1428 | Kron & Chase, 1993 | L12608 | 13A, B |
| *Tilia americana* L. | Tiliaceae | *Alverson s.n*, WIS | 27-1428 | Chase et al., 1993 (Karol) | | 10B |
| *Tovaria pendula* Ruiz & Pav. | Tovariaceae | *Smith & Smith 1831*, WIS | 27-1428 | Rodman et al., 1993 | M95758 | 10A, B |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Trapa natans* L. | Trapaceae | none | 27-1428 | Conti et al., 1993 | L10226 | 11C |
| *Platytheca verticellata* Baill. | Tremandraceae | *M. W. Chase 179*, NCU | 29-1428 | Chase et al., 1993 (Chase) | L01944 | 11A, C |
| *Trigonia nivea* Cambess. | Trigoniaceae | *W. R. Anderson 13656*, MICH | 31-1428 | Chase et al., 1993 (Chase) | | 11A, B |
| *Trochodendron aralioides* Siebold & Zucc. | Trochodendraceae | *Qiu 90026*, NCU | 29-1428 | Albert et al., 1992b (Qiu) | L01958 | 7A, B, 16 |
| *Tropaeolum majus* L. | Tropaeolaceae | *M. W. Chase 113*, NCU | 27-1428 | Price & Palmer, 1993 | L14706 | 10A, B |
| *Typha latifolia* L. | Typhaceae | *Bradley 24974*, GMUF | 32-1428 | Duvall et al., 1993 (Duvall) | M91634 | 6A, B |
| *Typha latifolia* L. | Typhaceae | *Kress 90-3170*, US | 31-1374 | Smith et al., 1993 | L05464 | |
| *Celtis yunnanensis* C. K. Schneid. | Ulmaceae | *Qiu P90002*, NCU | 27-1428 | Chase et al., 1993 (Qiu) | L12638 | 11A, B, 16 |
| *Trema micrantha* Blume | Ulmaceae | *M. W. Chase 335*, NCU | 27-1428 | Chase et al., 1993 (Qiu) | | 11B, 16 |
| *Boehmeria nivea* (L.) Gaudich. | Urticaceae | *Qiu 91049*, NCU | 27-1428 | Chase et al., 1993 (Qiu) | | 11B, 16 |
| *Valeriana officinalis* L. | Valerianaceae | *Jansen 909*, MICH | 1-1428 | Olmstead et al., 1992 (Michaels) | L13934 | 14A, B |
| *Vellozia* sp. | Velloziaceae | unknown | 47-1428 | Duvall et al., 1993 (Clark) | | 5A, B |
| *Callicarpa dichotoma* (Lour.) K. Koch | Verbenaceae | *Olmstead 88-012*, COLO | 103-1428 | Olmstead et al., 1993 | L14393 | 15A, B |
| *Clerodendrum fragrans* Hort ex Vent. | Verbenaceae | Matthaei BG 840210 (U Michigan) | 103-1428 | Olmstead et al., 1992 | L11689 | 15A, B |
| *Verbena bonariensis* L. | Verbenaceae | none | 103-1428 | Olmstead et al., 1993 | L14412 | 15A, B |
| *Viola sororia* Willd. | Violaceae | none | 103-1428 | Olmstead et al., 1992 | L11674 | 11A, B |
| *Phoradendron serotinum* (Raf.) M. C. Johnst. | Viscaceae | *Nickrent 2077*, ILL | 31-1407 | Morgan & Soltis, 1993 | L11199 | 9B, 12A |
| *Vitis aestivalis* Michx. | Vitaceae | *M. W. Chase 226*, NCU | 27-1428 | Albert et al., 1992b (Chase) | L01960 | 9A, 12B |
| *Qualea* sp. | Vochysiaceae | *W. R. Anderson 13660*, MICH | 31-1428 | Olmstead et al., 1992 (Chase) | | 10A, 11C |
| *Welwitschia mirabilis* Hook. f. | Welwitschiaceae | none (U California Riverside) | 1-1428 | Chase et al., 1993 (Furnier) | | 3A, B |
| *Belliolum* sp. | Winteraceae | *Qiu 90025*, NCU | 29-1428 | Qiu et al., 1993 | L12633 | 4B |
| *Drimys winteri* J. R. & G. Forster | Winteraceae | *Qiu 90016*, NCU | 29-1428 | Albert et al., 1992b (Qiu) | L01905 | 4A, B |
| *Tasmannia insipida* DC. | Winteraceae | *A. N. Rodd 5540*, NSW | 27-1428 | Albert et al., 1992b (Qiu) | L01957 | 4B |
| *Xanthorrhoea hostilis* R. Br. | Xanthorrhoeaceae | *M. W. Chase 192*, NCU | 29-1428 | Duvall et al., 1993 (Chase) | | 5A, B |
| *Bowenia serrulata* (W. Bull) Chamb. | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | L12671 | 3A, B |
| *Ceratozamia miqueliana* H. Wendl. | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | | 3A |
| *Chigua restrepoi* D. W. Stev. | Zamiaceae | unknown | 31-1428 | Chase et al., 1993 (Hills & Chase) | | 3A, B |
| *Dioon spinulosa* Dyer | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | | 3A, B |
| *Encephalartos arenarius* R. A. Dyer | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | L12676 | 3A, B |
| *Lepidozamia hopei* Regel | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | | 3A |
| *Macrozamia communis* (F. Muell.) L. A. S. Johnson | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | | 3A |
| *Microcycas colocoma* (Miq.) DC. | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | | 3A |
| *Stangeria eriopus* (Kunze) Baill. | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | | 3A, B |
| *Zamia inermis* Vovides, J. D. Reese & M. Vásquez-Torres | Zamiaceae | *Schutzman s.n.*, FLAS | 31-1428 | Chase et al., 1993 (Hills & Chase) | L12683 | 3A, B |
| *Globba curtisii* Holttum | Zingiberaceae | *Kress & Beach 87-2161*, SEL | 31-1374 | Smith et al., 1993 | L05499 | 6A, B |
| *Hedychium flavum* Roxb. | Zingiberaceae | USBG 90-653 | 31-1374 | Smith et al., 1993 | L05450 | |

APPENDIX. Continued.

| Species | Family | Voucher/source | Sequence* | Literature citation† | Database accession‡ | Figure in Chase et al., 1993§ |
|---|---|---|---|---|---|---|
| *Hedychium gardnerianum* Ker Gawl. | Zingiberaceae | *Bradely 24975*, GMUF | 32-1351 | Duvall et al., 1993 (Duvall) | M91628 | 6A, B |
| *Riedelea* aff. *wrayii* | Zingiberaceae | *Marie Selby BG 83-203*, SEL | 31-1374 | Smith et al., 1993 | L05460 | 6A, B |
| *Zingiber gramineum* Noronha | Zingiberaceae | *Kress 91-3266*, US | 31-1374 | Smith et al., 1993 | L05465 | 6A, B |
| *Guaiacum sanctum* L. | Zygophyllaceae | *W. R. Anderson s.n.*, MICH | 31-1428 | Chase et al., 1993 (Chase) | | 11A, B |

* Amount of sequence used in 499-taxon analysis only (in some cases more incomplete sequences were used in 475-taxon analysis, Chase et al., 1993; note that some taxa were used only in studies other than Chase et al., 1993).

† Publication in which an *rbc*L sequence for this taxon was first cited. If this sequence was produced by someone other than one of the authors of the cited paper, then this person's name is listed in parentheses after the publication. In cases for which there are large numbers of authors, the specific author who produced the sequence is given in parentheses.

‡ Accession numbers prefixed by "D," "M," or "L" are GenBank; those with "X" are EMBL.

§ If no figure number is listed, then the taxon was included only in the cited publication (this issue) and not in Chase et al. (1993).

Abbreviations used: Arb., arboretum; BG, botanical garden; G, garden; Natl., national; RBG, Royal Botanic Gardens; Trop., tropical; U, university; USBG, United States Botanical Garden; herbarium acronyms are the standard ones.



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# NOTICE

## The Rupert Barneby Award

The New York Botanical Garden is pleased to announce that David Clarke, of the University of Illinois, Urbana, is the recipient of the 1992 Rupert Barneby Award. Mr. Clarke will use the award to complete a taxonomic treatment of *Acacia* series *Gummiferae* of the Caribbean, both as a part of his graduate thesis and as a contribution to the flora of the Greater Antilles.

The New York Botanical Garden also invites applications for the 1993 Rupert Barneby Award. The award of $1,000 is to assist researchers planning to come to the New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae and a letter describing the project for which the award is sought and how the collection at NYBG will benefit their research. Travel to NYBG should be planned between January 1, 1994, and January 31, 1995. The letter should be addressed to Dr. Enrique Forero, Director, Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126 USA, and received no later than December 3, 1993. Announcement of the recipient will be made by December 17. Anyone interested in making a contribution to The Rupert Barneby Fund in Legume Systematics, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Forero.

Volume 80, Number 3, pp. 523–786 of the Annals of the Missouri Botanical Garden
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# Symposium Proceedings Published in Recent Issues of the *Annals of the Missouri Botanical Garden*

## Phylogeny of Asteridae

*Annals of the Missouri Botanical Garden* 79(2) (Spring 1992). The monophyly, sister group (or groups), and patterns of relationships of the Asteridae are discussed in the symposium "Phylogeny of Asteridae," organized by Larry Hufford of the University of Minnesota. The symposium was jointly sponsored by the American Society of Plant Taxonomists and the Botanical Society of America and was held at their annual meeting, 7 Aug. 1990, in Richmond, Virginia. 238 pages. $27.00, plus postage.

## The Lycopsida: A Symposium

*Annals of the Missouri Botanical Garden* 79(3) (Summer 1992). This symposium discusses the unique phylogenetic position and morphological distinctness of the Lycopsida; these are used as vehicles to study convergent structural evolution in vascular plants or limits on structural solutions to common problems such as light interception, propagule dispersal, and nutrient acquisition. The symposium was organized by William A. DiMichele and Judith E. Skog and was jointly sponsored by the Paleobotanical Society of America and the American Fern Society. The symposium was held on 8 Aug. 1989 as part of the American Institute of Biological Sciences meetings held in Toronto, Canada. 289 pages. $30.00, plus postage.

## Knowledge Brokering: The Mechanics of Synthesis

*Annals of the Missouri Botanical Garden* 80(2) (Spring 1993). This symposium, the 38th Annual Systematics Symposium of the Missouri Botanical Garden (held 4–5 Oct. 1991, in St. Louis, Missouri), discusses the value and future necessity of assimilating diverse biological information into new and broader syntheses, taking advantage of computer-based data-management systems. 41 pages (entire issue 230 pages). $35.00, plus postage.

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**Cover illustration.** *Pleurothyrium giganthum* van der Werff, by J. Myers.

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# SYSTEMATICS OF *RUELLIA* (ACANTHACEAE) IN SOUTHERN SOUTH AMERICA[1]

*Cecilia Ezcurra*[2]

ABSTRACT

*Ruellia* comprises 23 species in southern South America, which display great diversification in flower and inflorescence morphology, presumably associated with a wide array of pollinators; this has resulted in the evolution of many different floral syndromes. It is suggested that this diversification could have evolved through heterochronic developmental changes associated with cleistogamy that produce morphological variation in flower form, selected by different types of pollinators. The generic limits of *Ruellia* are discussed in relation to this variation, and several generic names are considered synonyms, including *Penstemonacanthus*. Seven informal taxonomic groups of species are delimited: *Chiloblechum*, *Dipteracanthus*, *Ebracteolati*, *Hygrophiloidei*, *Physiruellia*, *Ruellia*, and *Salpingacanthus*. Within these, *Ruellia magniflora* is described as new, and more than 20 specific and subspecific names are treated as synonyms for the first time. *Ruellia lanceolata* is excluded from the genus and reduced to synonymy in *Justicia*. The species are described and illustrated, and keys to all the taxa are given.

*Ruellia*, one of the largest genera of the Acanthaceae, consists of approximately 250 species of perennial herbs, subshrubs, and shrubs, with a largely tropical and subtropical distribution. The New World is the most important center of diversity for this genus, especially with regard to inflorescence pattern and corolla morphology. This variation is probably correlated with selective pressures of a wide array of different types of pollinators, which have resulted in a great diversification of pollination syndromes.

Many of the North and Central American spe-

[1] I am grateful to the directors and curators of the herbaria mentioned for the loan of herbarium material and photographs or photocopies of types. Special thanks are given to Dick Brummit and Dieter Wasshausen for generous help during my stays at K and US, and to the many other people that collaborated with me during visits to herbaria. I very much appreciate the comments of Fernando Zuloaga and two anonymous reviewers on the manuscript. I also thank Vladimiro Dudas for the skillful line drawings, and all the friends and colleagues of Instituto Darwinion, San Isidro, and Laboratorio Ecotono, C.R.U.B., Bariloche, who provided helpful discussion or assistance in the preparation of this paper. I acknowledge Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina for financial support, the Smithsonian Institution and Missouri Botanical Garden for short visit grants that allowed me to study Acanthaceae collections in North American herbaria, and the American Society of Plant Taxonomists for an award that financed my visits to herbaria of São Paulo and Rio de Janeiro, Brazil.

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cies have been treated in local revisions, but the species in South America have only been included in a few regional floras and have never been the subjects of modern revisionary work. The number of species in the Americas is probably the largest in all continents, easily exceeding 100, and many of them have ornamental value because of their handsome, large, colorful flowers. The diversity in flower morphology has previously led to much confusion as to generic delimitation and sectional classification, but this variation also makes *Ruellia* an interesting model for the study of evolution of pollination syndromes.

The most recent overall taxonomic treatment of the genus, the subgeneric classification of Lindau (1895) in Engler & Prantl's *Die Natürlichen Pflanzenfamilien*, is currently inadequate when one takes into account the diversity encountered in the Neotropics. Nearly a century has elapsed since Lindau's works on the family (see Loesener (1924) for a complete list), and the many new specimens that have been collected in the New World since his death provide additional data on the morphology, variation, and distribution of the species.

This systematic treatment represents only a preliminary approach to the understanding of the neotropical taxa of this large and diverse genus. Although considerable study on a worldwide basis is needed to produce a more robust and permanent infrageneric classification of *Ruellia*, this revision, which covers southern South America and includes 23 species divided into seven groups on the basis of morphological affinity, is intended to encompass much of the diversity of the genus in the Neotropics. When extending the study to the rest of the Americas, corrections and additions may be necessary, but it is expected that this classification shall remain as a basic framework for future studies.

Most of the previous treatments, being of a regional character, have covered only a small portion of the ranges of the species. This has resulted in the proliferation of names associated with different regions, which in many cases are synonyms. This study therefore also aims to correctly delimit the species in the area and to clarify their nomenclature.

## Materials and Methods

This treatment covers Argentina, southern Brazil (states of Paraná, Santa Catarina, and Rio Grande do Sul), Paraguay, and Uruguay. Although this is a politically limited area, it is representative of all the neotropical floristic regions found in southern South America and includes nearly the entire basins of the rivers Paraná, Uruguay, and De la Plata, along with their tributaries. This implies that it is a geographically more or less isolated region, physically separated by watersheds from other basins in South America.

Although the present study is based mainly on herbarium material, live populations of most of the species were studied during collecting trips to northern Argentina in 1984 (with M. Ponce and A. Brown), 1985 (with R. Kiesling et al.), and 1986 and 1989 (with F. Zuloaga et al.). More than 1,000 specimens from the following herbaria were studied: AA, BA, BAB, BM, CTES, G, GH, HAS, HBR, ICN, K, LIL, LP, MBM, MO, MVFA, NY, P, PACA, PKDC, R, RB, SI, SP, SPF, US. Type specimens or photographs of types from other herbaria (e.g., BR, GOET, GZU, LE, M, W, S) were requested, or studied at US where some were on loan. In several cases, only a selection of specimens representative of the distribution and diversity of the species are cited, because the collections studied are too numerous.

The nomenclature of phytogeographical regions follows Cabrera in Cabrera & Willink (1980). Cabrera's floristic approach to phytogeographical classification has been preferred to a more physiognomic treatment such as Hueck's (1978), because the floristic composition is believed to be more related to the evolutionary history of the vegetation in an area.

Regarding hybridization, the most important character used in this work to recognize naturally occurring hybrids is morphological intermediacy between two known species, either in plants in the field or in herbarium specimens. Additionally, the sympatric occurrence of the presumed parental species in the same area as the putative hybrid was taken into account. In some cases decreased pollen viability has also been accepted as a criterion of hybridization by studying pollen stainability with anilin blue in lactophenol.

One of the major problems encountered during this work has been that the majority of names of taxa of Acanthaceae from southern South America were proposed by Nees (1847a, b), who did not formally designate nomenclatural types for them. In the case of species, he referred to the specimen or list of specimens he had studied and considered representative. Here no lectotypes have been designated from the syntypes when more than one specimen was cited, because in most species I have not had direct access to the whole set of syntypes,

as this material is generally found in several different European herbaria.

In the cases of species where Nees proposed several infraspecific taxa, he designated them with Greek letters. As he generally considered only one infraspecific rank, these should be regarded as varieties, following Article 35.3 of the *International Code of Botanical Nomenclature* (Greuter et al., 1988). In some descriptions he named and described an *alpha* variety and cited material for it, in which case no material is cited for the name of the species. In these situations the holotype (or syntypes) of the name of the species is here assumed to be that specimen (or specimens) cited under the infraspecific taxon designated with the Greek *alpha*. This assumption is based on the fact that in most cases of species with several infraspecific epithets, Nees only named and described alternative varieties *beta*, *gamma*, *delta*, *epsilon*, etc., and when listing the material of the species, he referred to the *alpha* variety as that described under the specific epithet, in the general description (e.g., *Arrhostoxylon affine* Nees, 1847a: 59).

In a few cases he did not refer to an *alpha* variety (e.g., *Dipteracathus macranthus* Nees, 1847a: 37) when citing material, but just listed in the first place the specimens he regarded as representative of the species, and secondly those representative of varieties *beta* or *gamma*, etc. In those cases it is clear that the holotype of the species is the specimen cited in relation to the description of the species, and the material listed for infraspecific taxa *beta*, *gamma*, *delta*, *epsilon*, etc. is excluded.

## Taxonomic History and Generic Delimitation

The complex taxonomic history of *Ruellia* has been discussed in detail by Long (1964, 1973). The following is only a summary of the prevailing ideas on the delimitation of *Ruellia* through time.

*Ruellia* was established by Linnaeus (1737), who included eight species in his *Species Plantarum* (1753), of which *Ruellia tuberosa*, a tropical American perennial herb with blue flowers, was chosen as lectotype (Britton & Brown, 1913: 241). Nees (1847a), who treated the Acanthaceae of South America for Martius's *Flora Brasiliensis* and the family on a worldwide basis for the *Prodromus* of De Candolle (Nees, 1847b), placed the species described by Linnaeus in various genera. He even described more new genera to accommodate the numerous different but morphologically related variations he encountered in the tropics, especially in the New World. Oersted (1854), who worked on the Acanthaceae of Central America, also treated the species in several separate genera.

Bentham (1876) established the now mostly accepted circumscription of the genus by "sinking" 18 genera, most of them described by Nees, into *Ruellia*. Lindau (1895) followed Bentham, including in *Ruellia* more than 100 species classified in 9 sections. This wide concept has been accepted by most modern authors.

The New World species have generally been treated in the broad generic sense, especially in North and Central America (e.g., Daniel, 1990; Durkee, 1978, 1986; Gibson, 1974; Leonard, 1936; Long, 1970; Tharp & Barkley, 1949; Turner, 1991; Wasshausen, 1966). In South America most authors have also followed Bentham and Lindau treating *Ruellia* in its wider sense (e.g., Chodat & Hassler, 1903; Dawson, 1979; Ezcurra, 1989; Ezcurra & Wasshausen, 1992; Leonard, 1951–1958; Lillo, 1937; Lindau, 1894; Rambo, 1964; Wasshausen & Smith, 1969). But perhaps because of the bewildering diversity that can be found in the tropics of South America, especially with respect to flower and inflorescence morphology, some authors have gone back to Nees' ideas in this area (Bremekamp, 1938, 1969; Bremekamp & Nannega Bremekamp, 1948; Rizzini, 1949). The result has been that some species names in *Ruellia* have recently been treated once again in combination with names of genera previously considered synonyms, such as *Arrhostoxylum* Nees (Bremekamp, 1969) and *Stephanophysum* Pohl (Bremekamp, 1938, 1969; Barker, 1986), or with new names, such as *Ulleria* Bremek. (Bremekamp, 1969).

This problem has led to the series of biosystematic works of Long (e.g., 1966, 1973, 1975, 1976a, b) that, through field studies, crossing experiments, and chromatographic comparisons of corolla pigments, have aimed to establish the relative taxonomic position of several species within *Ruellia* sens. lat., and at the same time provide an insight to the most natural circumscription of the genus. These works, together with the cytogenetic studies on the family performed by Grant (1955), Daniel et al. (1984, 1990), and Piovano & Bernardello (1991), generally support the idea that *Ruellia* consists of a large and morphologically diversified group of more or less phylogenetically related species, with one constant chromosome number, in which natural hybridization is frequent between closely related species.

In this treatment *Ruellia* is treated "sensu lato," being characterized by the generally large and showy, subactinomorphic flowers, the four, fre-

quently didynamous stamens, the oblong, symmetrical, basally rounded anthers, the spherical, porous, coarse-reticulate pollen, and the (2–)4–numerous-seeded capsules, with the placentas remaining attached to the walls at maturity (separating in a few species).

### Intrageneric Relationships

The most recent comprehensive treatment of *Ruellia*, Lindau's (1895) synopsis, separated the genus into nine sections, of which only five were considered by Lindau as "typical." Of these five, three of them included the majority of the species known at that time: *Euruellia* (which included species classified by Nees (1847b) as *Cryphiacanthus* Nees and *Ruellia* L. pro parte), *Dipteracanthus* (which included *Ophtalmacanthus* Nees, and *Dipteracanthus* Nees groups *Hygrophiloidei*, *Calycosi*, and *Genuini*), and *Physiruellia* (which included *Aphragmia* Nees pro parte, *Arrhostoxylon* Nees, *Dipteracanthus* Nees pro parte, *Siphonacanthus* Nees, *Stemonacanthus* Nees, and *Stephanophysum* Pohl). Most of the others were monotypic sections, created mostly to accommodate species of uncertain position. The characters he used in the delimitation of groups were capsule morphology and corolla shape. In this synopsis Lindau noted that both the delimitation of the species and the separation of the genus into sections were difficult in *Ruellia* because of the extraordinary richness he encountered in form, and that his classificatory scheme was provisional.

Recently, Ramamoorthy (1991, 1992) described two new sections from Mexico, *Chiropterophila* and *Urceolata*, mostly characterized by flower morphology; capsule structure was not taken into account.

In this treatment, the species are classified into groups without formal taxonomic recognition, principally on the basis of capsule structure correlated with inflorescence morphology. Corolla shape appears to have frequently been subject to rapid diversification through disruptive selection by different pollinators. This appears to have produced many parallel events in the evolution of the genus, i.e., homoplasies, and therefore this character is treated as secondary in group delimitation.

Although this classification is also provisional because it takes into account only a fraction of the species of the genus (probably less than 15%), this fraction is quite representative of the diversity of *Ruellia* encountered in the New World, as seen in the neotropical collections studied. But some important groups of species, such as those considered by some authors (e.g., Long, 1976b) as *Aphragmia* Nees (= *Dipteracanthus* group *Aphragmia* Nees, 1847a; *Dipteracanthus* group *Paniculati* Nees 1847b; *Ruellia* sect. *Physiruellia* group *Glandulosae* Lindau, 1895), are not represented in the area studied, and therefore have not been included. Thus the formal taxonomic position and rank of the groups will have to be worked out once all the species are taken into account on a worldwide basis.

### Morphology

*Habit.* Most of the species are perennial herbs or subshrubs, more rarely shrubs or small trees, the majority erect, sprawling, decumbent or prostrate, except a few semiscandent or rosettiform species. All have a basal rhizome with more or less thick, fibrous roots, and sometimes adventitious roots are also produced in decumbent branches where the nodes touch the ground. The young stems are frequently quadrangular, in some species more markedly so, in others subterete, and in some of group *Physiruellia* the regions over the nodes are swollen and geniculate. The swollen region fractures easily and may be important in the vegetative propagation of the plants by stem division.

*Leaves.* Leaves are opposite and generally petiolate, and only a few species (of group *Ruellia*) present leaves in rosettes. The blades are simple, with the margin entire, crenulate or crenate, more rarely dentate. The surfaces are pubescent or glabrate. The leaves sometimes intergrade into bracts toward the stem apices. Venation is pinnate, but, in the upper leaves transformed into bracts in some species of group *Chiloblechum*, the inferior secondary veins arise near or at the base of the blade, producing a subpalmate appearance.

*Indument and surface.* The trichomes in *Ruellia*, like in most Acanthaceae (Ahmad, 1978; Karlström, 1978), are of two types: glandular, with a sessile or stalked multicellular head, and eglandular, simple and uniseriate (Fig. 1A). Different types of pubescences can occur together in different proportions. In some species multicellular, sessile, disk-shaped or "patelliform" (Daniel, 1990) glands appear like small punctations on the surface of leaves, bracts, and calyx lobes (Fig. 1B). These glands are frequent in tropical and subtropical species of different taxonomic groups from open areas, such as *Ruellia bulbifera*, *R. coerulea*, *R. erythropus*, or *R. multifolia*, and could act as extrafloral nectaries secreting substances to attract ants.

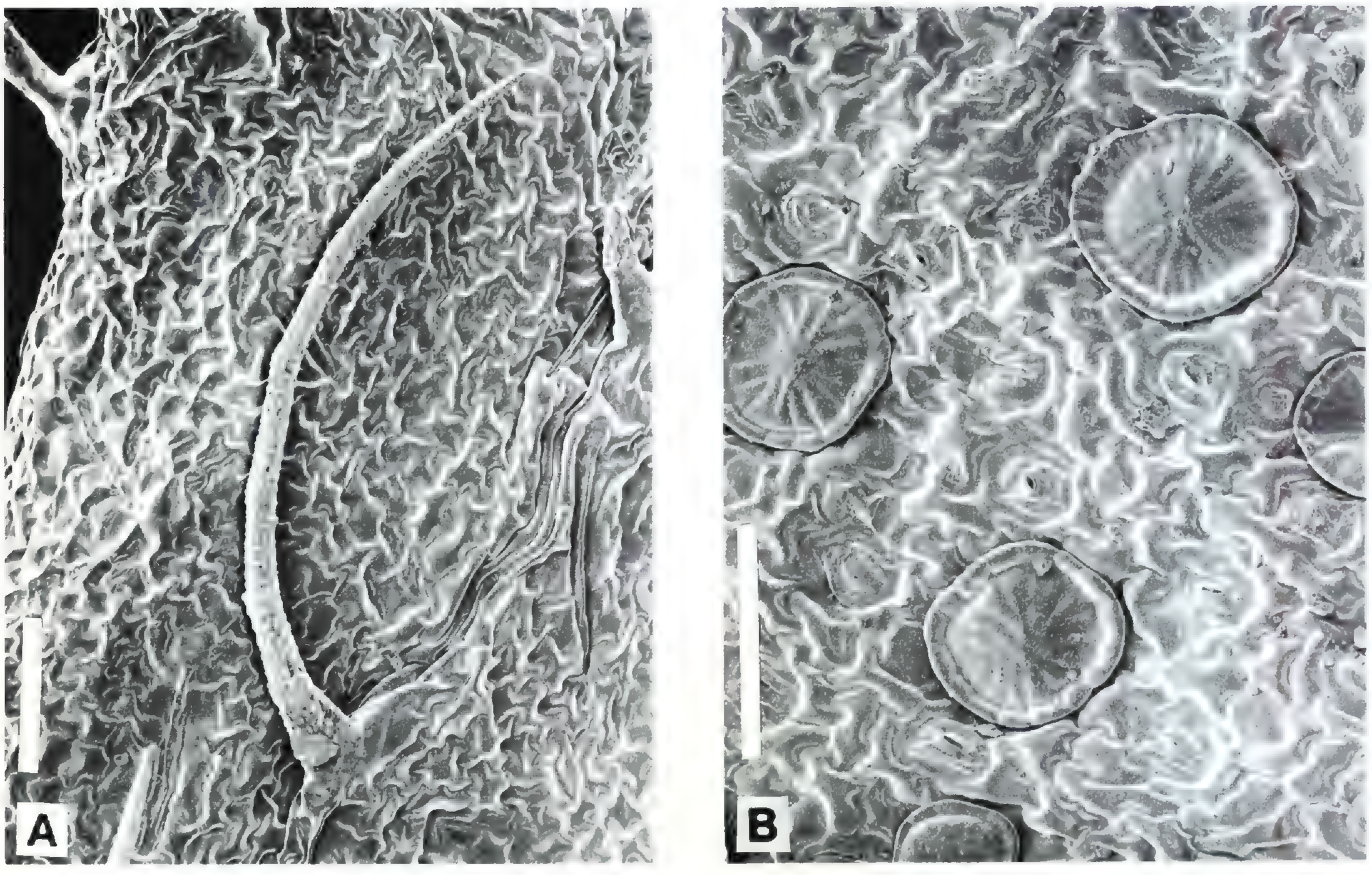


FIGURE 1. Indument of *Ruellia*. —A. Simple, uniseriate hair. —B. Sessile, patelliform glands. (SEM photographs from bract surface of *R. erythropus*, *Pensiero 1580*. Scale bar = 100 μm.)

Cystoliths are small mineral (calcium carbonate) concretions in the interior of epidermal cells and are present in most genera of Acanthaceae. In *Ruellia*, on the surfaces of vegetative organs, in dry material, the cystoliths appear as small, linear, more or less prominent structures, sometimes resembling appressed, strigose pubescence. In live material they are much less readily apparent.

*Inflorescence.* The basic inflorescence pattern in *Ruellia* consists of simple or compound dichasia that appear as lateral elements of the indeterminate axes (Sell, 1969a). Within this basic scheme, several variations that generally characterize different groups of related species can be found.

In groups *Physiruellia* and *Ruellia* the dichasia are often compound and pedunculate, forming multiflowered axillary cymes (Fig. 2A, B). These are sometimes condensed into terminal thyrses, especially in the latter group, producing an upper floral region differentiated from the purely vegetative basal region by modification of the terminal leaves into small bracts (Fig. 2B). In group *Hygrophiloidei* the dichasia are generally reduced to a more or less pedunculate solitary flower with two bracteoles, in the axils of the terminal leaves. In many of these cases the inflorescences are anisophyllous, i.e., only one cyme appears in each node, alternating sides (Fig. 2A).

In group *Dipteracanthus*, the dichasia are always simple and sessile, generally reduced to axillary, solitary sessile flowers with two bracteoles, these always subtended by the upper leaves (Fig. 2C). In groups *Salpingacanthus* and *Ebracteolati* the flowers also appear sessile and solitary in the axils of the upper leaves, but the reduction is even greater as the bracteoles are extremely reduced or absent (Fig. 2D). In group *Chiloblechum* the sessile flowers without bracteoles are grouped into a four-sided spike, the upper leaves generally being somewhat modified into sessile bracts (Fig. 2E). In this work, the correlation between inflorescence and capsule structure is used to define groups.

*Calyx.* In *Ruellia* the calyx is always five-parted, but in group *Salpingacanthus* and in some species of group *Chiloblechum* (e.g., *Ruellia erythropus*) the two lateral lobes are fused to the inferior ones, and thus a more or less three-lobed structure is formed.

*Corolla.* The corolla consists of a narrow basal tube, a more or less cylindrical, infundibuliform or campanulate throat, with the limb parted into two

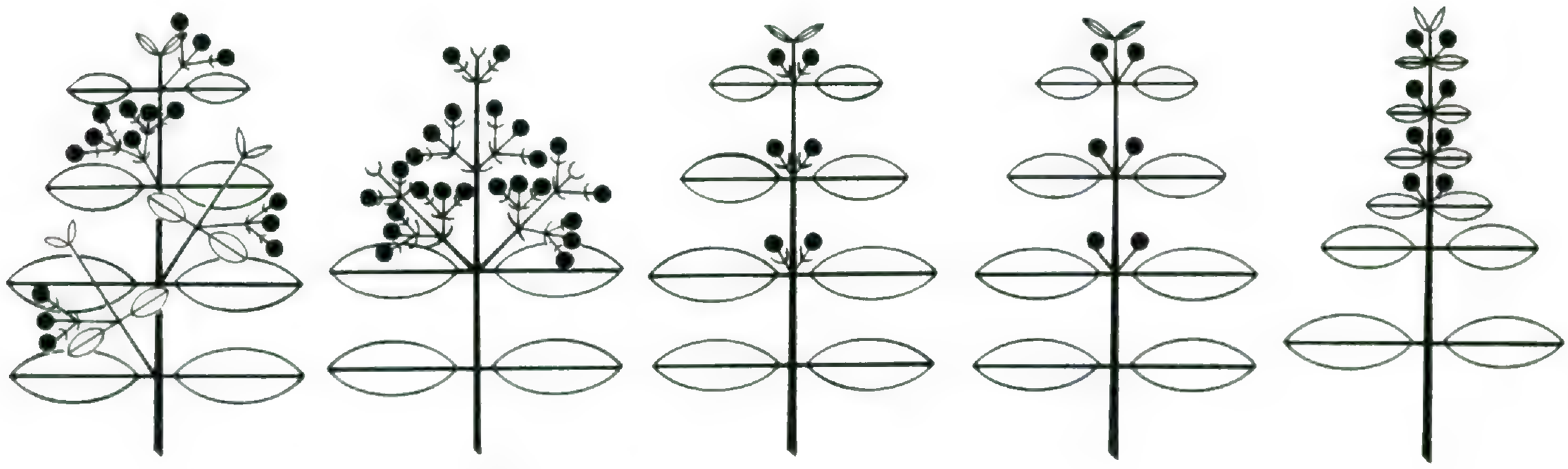


FIGURE 2. Inflorescence types in *Ruellia*.—A. *R. angustiflora* (group *Physiruellia*).—B. *R. ciliatiflora* (group *Ruellia*).—C. *R. multifolia* (group *Ruellia*).—D. *R. geminiflora* (group *Ebracteolati*).—E. *R. erythropus* (group *Chiloblechum*). (Schematic, from herbarium material.)

posterior and three anterior lobes more or less similar in size and shape, thus rendering it subactinomorphic in a basically zygomorphic family. This basic structure is widely modified in different species. The color also varies from blue, mauve, pink, red, and yellowish, to white. The lower part of the throat and/or the base of the anterior lobes is often marked with colored streaks or veins that probably function as nectar guides. Corolla morphology seems very plastic in *Ruellia* and has probably been subject to diversification due to the action of different pollination agents, even within groups of otherwise closely related species. The different sets of morphological characteristics of the flowers are here described in relation to presumed pollinating agents, as pollination syndromes.

Although there is no strict correlation between the different morphological types of corolla and the different groups, some types are present more often in some groups than others. The following classification is somewhat similar to that proposed by Barker (1986) for flower morphology of Australian Acanthaceae in general.

*Red tube flowers* (presumably pollinated by hummingbirds: ornithophilous) (Fig. 3A, B). The corollas are frequently horizontal or pendulous and red, the basal tube and the throat form a more or less narrow tube, sometimes anteriorly inflated, and the lobes are generally small and erect or semierect. This morphological type generally appears associated with multiflowered axillary cymes as inflorescences, with the peduncles and pedicels frequently weak. It is frequent in group *Physiruellia* (e.g., *Ruellia angustiflora*, *R. elegans*).

*Mauve or blue infundibuliform flowers* (presumably pollinated by large bees: melitophilous) (Fig. 3C–F). The basal tube is short, the corollas are blue or mauve and functionally zygomorphic, i.e., generally angled and tilted, with marked palate rib markings in the lower part of the throat, and with the lower lobes with nectar guides in the base. This type is common in groups *Ruellia*, *Dipteracanthus*, and *Ebracteolati* (e.g., *Ruellia ciliatiflora*, *R. brevicaulis*, *R. geminiflora*).

*White trumpet flowers* (presumably pollinated by

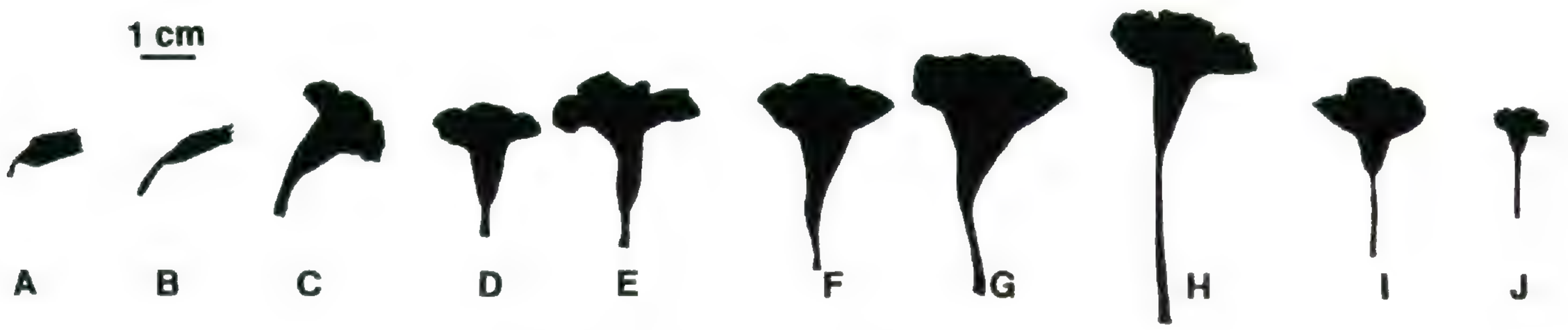


FIGURE 3. Corolla morphology in *Ruellia*. A, B. Red tube ornithophilous flowers.—C–F. Mauve or pale blue infundibuliform melitophilous flowers.—G, H. White trumpet sphingophilous flowers.—I, J. Blue hypocrateriform psychophilous flowers. (Photocopied from herbarium material: A, *R. brevifolia*; B, *R. angustiflora*; C, *R. ciliatiflora*; D, *R. bulbifera*; E, *R. geminiflora*; F, *R. brevicaulis*; G, *R. multifolia*; H, *R. macrosolen*; I, *R. erythropus*; J, *R. hypericoides*.)

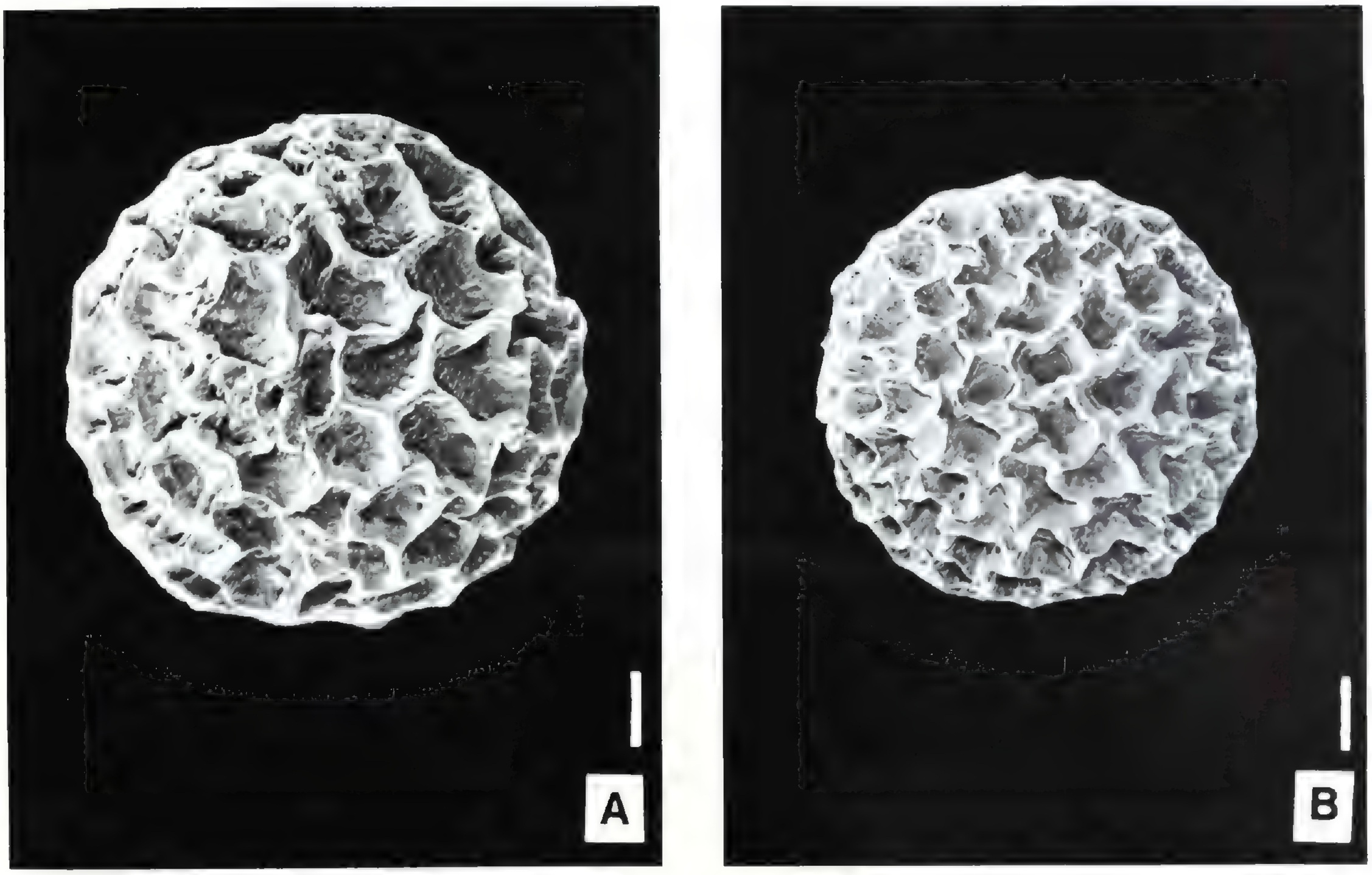


FIGURE 4. Pollen of *Ruellia*.—A. *R. coerulea* (*West 8472*).—B. *R. hypericoides* (*Zuloaga 3248*). (SEM photographs of unacetolized pollen grains. Scale bar = 10 μm.)

hawkmoths: sphingophilous) (Fig. 3G, H). The basal tube is very long, and the corollas are more or less erect, white or whitish, actinomorphic, lacking differential markings in the lobes. This type of flower appears in several unrelated groups present in southern South America, such as *Dipteracanthus*, *Ruellia*, and *Salpingacanthus* (e.g., *Ruellia multifolia*, *R. macrosolen*, *R. nobilis*), and has probably evolved independently many times within the genus.

*Blue hypocraterimorph flowers* (presumably pollinated by butterflies: psychophilous) (Fig. 3I, J). The basal tube is very narrow, and the corollas are erect, blue, and without clear differential markings in the lobes. This type appears in group *Chiloblechum* (e.g., *Ruellia hypericoides*, *R. erythropus*).

Additionally, several neotropical species present large, pale, greenish, dull-colored, campanulate flowers that have saccate corollas with a wide open throat and exserted stamens (e.g., *Ruellia petiolaris*, Daniel, 1990; *Ruellia* section *Chiropterophila*, Ramamoorthy, 1991) that appear to be pollinated by bats (chiropterophilous), but none with this syndrome reaches southern South America.

*Androecium*. In *Ruellia* there are four stamens which are generally didynamous, the two lateral being the shorter pair and the two anterior the longer, but the filaments are curved so that the anthers are placed under the posterior lobes, more or less deeply included or exserted. In ornithophilous species the stamens are sometimes all the same length. In all cases, the filaments are inserted below the throat of the corolla and are prolonged toward the interior and base of the corolla tube as two narrow protruding flaps that more or less separate the tube into a posterior (dorsal) section and an anterior (ventral) longitudinal channel.

*Pollen*. In the Acanthaceae, pollen morphology has traditionally been a useful taxonomic character in group delimitation at the generic and suprageneric level (Lindau, 1895; Petriella, 1968; Raj, 1961, 1973; Rizzini, 1949; Scotland, 1991). *Ruellia* species have spherical, porate, coarse-reticulate pollen (Fig. 4). Bremekamp & Nannega Bremekamp (1948) and Bremekamp (1969) suggested that differences in pollen morphology, such as sparsiporous grains versus three-porate ones, and differences in the constitution of the reticulum, such as size and regularity of the brochi, height of the muri, etc., could be used to separate the Old World species of *Ruellia* from the New World ones. In southern South American species the variations in size of the grains and in ornamentation of the walls

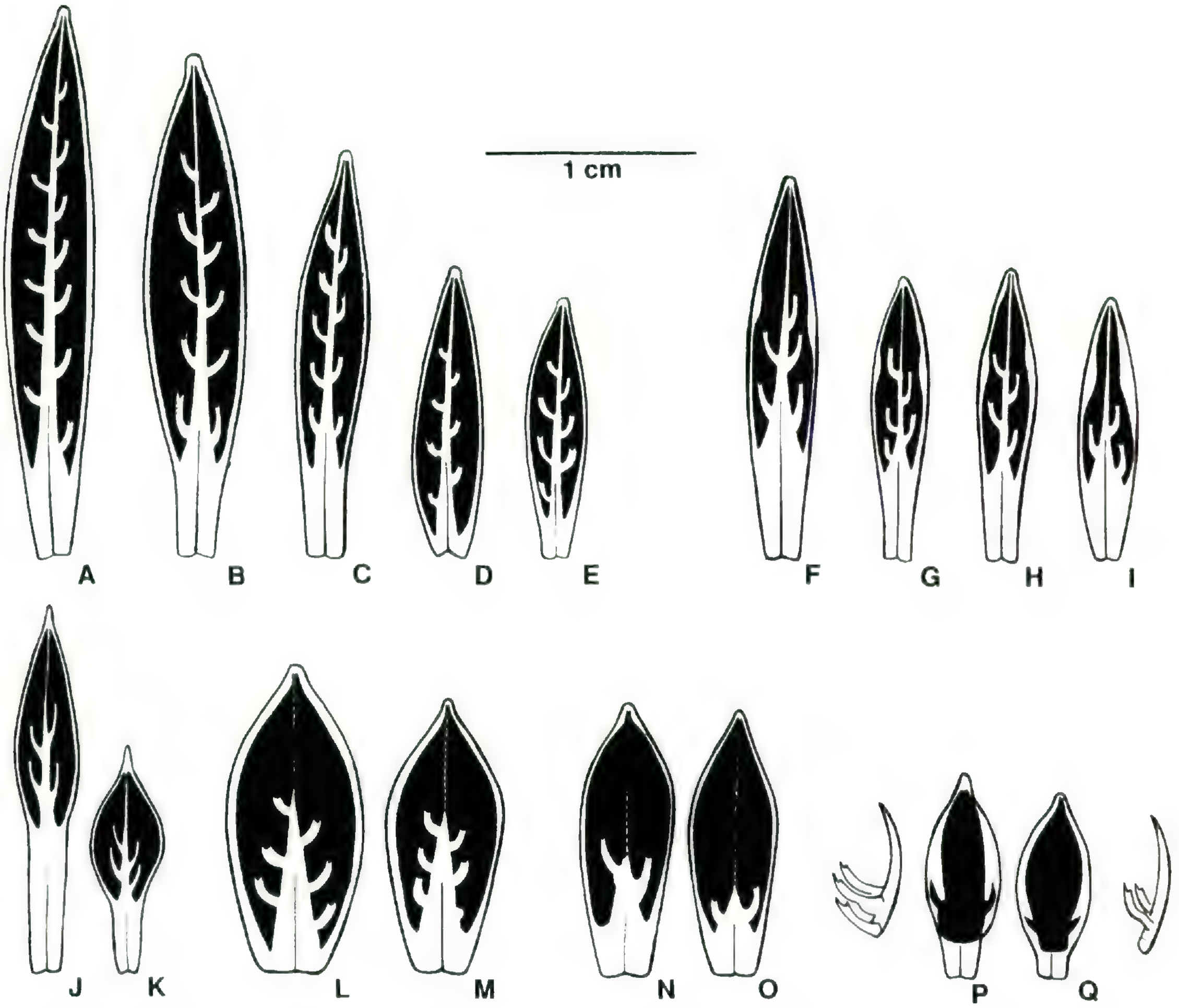


FIGURE 5. Capsule structure in *Ruellia*.—A–E. Group *Ruellia*.—F–I. Group *Physiruellia*.—J, K. Group *Hygrophiloidei*.—L, M. Group *Dipteracanthus*.—N, O. Group *Ebracteolati*.—P, Q. Group *Chiloblechum*. (Open calsules without seeds drawn with camera lucida, semischematic, from the same specimens used to illustrate the descriptions of the species. A, *R. coerulea*; B, *R. macrosolen*; C, *R. ciliatiflora* D, *R. morongii*; E, *R. hygrophila*; F, *R. angustiflora*; G, *R. brevifolia*; H, *R. longipedunculata*; I, *R. sanguinea*; J, *R. epallocaulos*; K, *R. kleinii*; L, *R. multifolia*; M, *R. brevicaulis*; N, *R. bulbifera*; O, *R. geminiflora*; P, *R. erythropus*; Q, *R. hypericoides*.).

do not correlate with any other morphological characters to help in the separation of groups of related species.

*Gynoecium*. The stigma is two-lobed with the lobes dorsiventrally compressed, the anterior lobe being generally larger than the posterior.

*Capsules*. In *Ruellia*, like in most Acanthaceae, the fruit is a biloculate, two-valved, loculicidal capsule. The base of the capsule is contracted and solid, and the seeds are found in the hollow upper part, subtended by hooklike retinacula. The different mechanisms by which the capsules open and the seeds are ejected are described by Sell (1969b). In some species of *Ruellia* the dehiscence is produced by the drying of the capsules (xerochasy), and in others by humidification (hydrochasy).

The structure of the capsule and the number of seeds per locule (1–14) are variable and are important taxonomic characters at a supraspecific level. Differences in the ratio between the length of the sterile, contracted, solid base, and the fertile, thicker, hollow upper part, characterize different groups of related species.

Group *Ruellia* (Fig. 5A–E) is characterized by the terete, narrowly elliptic capsules with a very short solid base (less than ¼ the length of the capsule) and numerous seeds per locule (5–14). Group *Physiruellia* (Fig. 5F–I) has a longer solid base in relation to the hollow part (⅓), and fewer seeds per locule (3–7). Group *Hygrophiloidei* (Fig. 5J–K) has clavate capsules with a short, rounded, apiculate hollow head of nearly the same length as the solid base, with very few seeds per locule (3–

4). Group *Dipteracanthus* (Fig. 5L, M) has terete, robust, thick-walled capsules with a short solid base (⅓ the length), and 3–6 seeds per locule. Group *Salpingacanthus* has a similar structure, with very large capsules. Group *Ebracteolati* (Fig. 5N, O) has an extremely reduced capsule with a very short solid base and only (1–)2 seeds per locule. Group *Chiloblechum* (Fig. 5P, Q) has small capsules with thin walls, a solid base ¼ the length, and 2–4 seeds per locule.

This last group differs markedly from the rest of the genus because on dehiscence, the protruding placentae with the retinacula and the seeds break away from the inner walls of each valve, separating elastically from the lower part of the capsule toward the top, and at the same time breaking the lateral walls. This type of dehiscence of the capsule has already been described for several unrelated genera within the family (e.g., *Dicliptera, Micranthus, Tetramerium, Blechum*) (Daniel, 1986; Sell, 1969b), but it is the first time it has been reported for *Ruellia*.

*Seeds.* The seeds are always flat and more or less orbicular in outline, with a slight notch at the chalazal end. The surface of the seed toward the outside of the capsule is usually convex, and the one toward the interior flat or concave. The seeds are more or less covered with appressed hairs that extend and turn mucilaginous on contact with water. This makes them extremely adhesive when wet, and in this way they can be dispersed by animals (ectozoochory). These hairs possess annular or spiral thickenings in their walls which strengthen their structure; the annular and spiral shape of the thickenings allows the hairs to lengthen on contact with water. In many species of group *Physiruellia* the hairs are condensed principally on the margins of the seeds, but otherwise the structure of the surface is quite constant. The mucilage the hairs secrete could also have a protective function, as it has shown high resistance to enzyme action (Lester & Ezcurra, 1991).

## Chromosome Numbers

The chromosome numbers of only less than 20% of the species of *Ruellia* have been studied, but they appear to be fairly uniform: more than 85% of the species are $2n = 34$ (Piovano & Bernardello, 1991). As Daniel et al. (1984) suggested, this constancy of chromosome number in all species of *Ruellia*, in contrast to the wide chromosomic variation that has been encountered in *Justicia*, the largest genus of the family, may be reflective of a more natural, though also large and morphologically diverse, taxon. The chromosome numbers of only eight of the species present in southern South America have been reported: *Ruellia brevifolia* (as *R. graecizans*) and *R. ciliatiflora* (as *R. lorentziana*) (Grant, 1955); *R. macrosolen* (Ezcurra & de Azkue, 1989); *R. bulbifera, R. coerulea* (as *R. tweediana*), *R. geminiflora, R. multifolia* var. *multifolia* (as *R.* aff. *dissitifolia*), and *R. longipedunculata* (Piovano & Bernardello, 1991).

Most *Ruellia* species have one pair of satellite chromosomes (Grant, 1955; Ezcurra & de Azkue, 1989; Piovano & Bernardello, 1991), and chromosome size seems quite variable (from 0.60 to 3.60 $\mu$m as reported by Piovano & Bernardello).

## Origin of Pollination Syndromes

The impressive morphological diversification of the flower in species of *Ruellia* from the New World suggests a limited set of morphological types. Distinct morphological flower types that appear recurrently within different genera and families of plants have traditionally been interpreted as representing pollination syndromes, i.e., the set of morphological, phenological, and physiological characters of flower and inflorescence that correlate with the morphology, behavior, and preferences of the effective pollinators of the species, and therefore represent adaptations to various modes of pollination (Ornduff, 1969). These different pollination syndromes have repeatedly been described for various taxonomic groups and have been summarized by Faegri & van der Pijl (1979) and Weberling (1989).

Even though Ornduff (1969) and Vogel (1991) cited several genera of gamopetalous families to exemplify complex patterns of adaptive radiation or divergence in floral morphology, few of them seem, as suggested by their morphological diversity, to have exploited such a diverse pollinator fauna as *Ruellia*. The diversity of floral form in this genus is similar to the adaptive radiation described by Grant & Grant (1965) for the Polemoniaceae and by Vogel (1991) for the Rubiaceae and Scrophulariaceae.

Cleistogamy in *Ruellia* is frequent (see Lord, 1981), and production of a great variety of floral morphs, from normal and reduced chasmogenes to semi-cleistogenes and cleistogenes, as has been described for the North American *Ruellia caroliniensis* (Long, 1971), suggests that floral morphology in the genus is labile, lacking developmental channelization. Different floral morphs within the same species have also been observed in cultivated specimens of the South American *Ruellia brevi-*

*folia* (Piovano et al., 1991), indicating developmental plasticity.

As summarized by Macnair (1989), in plant populations that are genetically variable regarding flower shape, size, coloration, or flowering time, different pollinator guilds can select different floral morphs. This can produce disruptive selection and result in the sympatric differentiation of species with different floral morphologies.

Differences in morphology related to different developmental stages can provide the variation on which selection can operate. This process has been suggested as the evolutionary origin of the corolla shape of the derived hummingbird-pollinated *Delphinium nudicaule* Torrey & Gray from a more generalized bumble-bee-pollinated species of *Delphinium*, through selection of neotenic forms by bird pollination (Guerrant, 1982).

This type of process, but through the selection of peramorphic instead of neotenic forms (as results of developmental acceleration or hypermorphosis), has been suggested to explain the evolution of *Ruellia macrosolen* (Ezcurra & de Azkue, 1989), a sphingophilous species with long, actinomorphic, white flowers, from sympatric and closely related melitophilous species, with shorter, functionally zygomorphic, blue flowers.

The heterochronic variability in development that has been observed in flower morphology within some species (expressed by the high frequency of cleistogamic and semicleistogamic or reduced forms), probably with a genetic basis, could thus be related to the wide array of floral syndromes in the genus. As has already been suggested (Ezcurra & de Azkue, 1989), the evolutionary shift from one floral syndrome to another may therefore have originated by simple heterochronic developmental changes selected by different pollinators.

## Reproduction and Dispersal

The role of cleistogamy in the reproductive biology of *Ruellia* has been discussed by Long (1971) in his detailed study of the floral polymorphy and breeding system of the North American *Ruellia caroliniensis*. Production of cleistogamic flowers has also been reported in many other genera of Acanthaceae, and Long has suggested that it is probably as important in this family as in Poaceae and Orchidaceae. Cleistogamic flowers in *Ruellia* are frequently inconspicuous structures with closed corollas of reduced size, difficult to differentiate from flower buds in herbarium material, but easily observed in live plants, where the capsules are produced without the opening of the flowers, and therefore present the closed corollas crowning the distal end, sometimes taking some time to fall off. In many cases the expression of cleistogamy has shown to have relation with external environmental factors (Uphof, 1938), like seasonality and environmental stress (Long, 1971; Piovano et al., 1991; Sell, 1977). This could explain the higher frequency of cleistogamic flower production in cultivated plants, especially in those transplanted to higher latitudes. This has been observed in plants of *Ruellia ciliatiflora* (Santos Biloni, 1963, as *R. lorentziana*) and *R. macrosolen* (Ezcurra & de Azkue, 1989) transplanted from northern Argentina (approximately 25°S) and cultivated in Buenos Aires (approximately 35°S lat.).

The combination of chasmogamic floral morphs well adapted to cross-pollination, with the production of reduced or cleistogamic ones in which autogamy is prevalent, serves as a means of assuring fertilization in cases where the efficiency of cross-fertilization decreases (Macnair, 1989). This is particularly so in cases of a single plant establishing itself in a new habitat, as is common in long-distance dispersal events, where generally one or a few seeds get introduced in a new area at a time. Moreover, colonizing plants frequently encounter a somewhat hostile environment in their new habitat, and the production of cleistogamic flowers in response to environmental stress, as is the case with *Ruellia*, ensures reproductive success with the minimum investment in flower production.

As Long (1976a) suggested, this succession of cycles of allogamy, with cycles of facultative autogamy that produce a whole series of homozygous biotypes, is probably the cause of many of the taxonomic problems present in *Ruellia*. Self-fertilization produces morphologically distinct local populations each with a low amount of diversity that can be erroneously identified as different species, and the outcrosses between different populations of this type can produce complex patterns of reticulate variation. Hence, the confused taxonomy of many *Ruellia* species groups may be related to these characteristics of the breeding system of the genus.

*Ruellia* seeds turn mucilaginous and adhesive on contact with water and in this way can be dispersed by animals (ectozoochory). Aquatic birds, especially migrating ones, could account for long-distance dispersal of such species as *Ruellia coerulea* and related entities of group *Ruellia* (e.g., *R. ciliatiflora*, *R. macrosolen*), which possess cylindrical capsules with numerous seeds and grow in open, disturbed, wet or seasonally flooded habitats. Although the distribution of the widespread and variable *Ruellia coerulea* is restricted to subtropical South America, there are species in south-

ern North America that seem closely related, such as *Ruellia malacosperma* and *Ruellia brittoniana* (cf. Turner, 1991). These could have originated by introductions through this process.

Stems fracture easily in the swollen regions over the nodes of many species, and this could also help in their dispersal. Decumbent stems of some species that grow in moist humus of the understory of forests root readily, and naturalized plants of *Ruellia brevifolia* in Instituto Lillo, San Miguel de Tucumán (Argentina), have been seen to reproduce in this way, resulting in dense thickets.

## Hybridization

Natural hybridization in *Ruellia* can be expected to be important in relation to two factors. First, many artificial crosses have resulted in hybrids, several with a high degree of fertility (Long, 1966, 1973, 1975, 1976a, b), suggesting that most species lack internal barriers to hybridization, especially when they are relatively closely related. Second, many species are sympatric in nature.

However, evidence for naturally occurring interspecific hybridization has been found only in a limited number of cases, and the putative hybrids (*Ruellia brevifolia* × *R. longipedunculata*, *R. brevicaulis* × *R. coerulea*) are discussed under the suspected parental species in the taxonomic section. The apparent rarity of natural hybrid production in the studied area may be due to the difficulties of recognizing them in herbarium material, especially between morphologically similar but variable species, and even in the field, when hybrid plant specimens or populations are rare and localized. Natural hybridization could therefore be underestimated, although it may have played an important role in the evolution of the genus. The existence of presumed naturally occurring hybrids between species pairs belonging to widely separated species groups (e.g., *Ruellia brevicaulis* × *R. coerulea*) suggests evolutionary reticulation, which could explain the taxonomic difficulties in delimiting supraspecific taxa within the genus.

It is also possible that sympatric species remain separated by external barriers, such as different pollinators, as has been suggested between *Ruellia macrosolen* and *R. ciliatiflora* (Ezcurra & de Azkue, 1989), or different ecological preferences in habitat, such as those between *Ruellia ciliatiflora* and *Ruellia coerulea*.

## Geographic Distribution and Habitat

*Ruellia*, being a mainly tropical genus, extends in South America to approximately 35°S and is present only in areas with floras belonging to the Amazon and Chaco floristic regions or dominions. In southern South America (from 20°S southward) these floristic regions have been subdivided into several phytogeographical provinces, each characterized by a different geography, climate, and vegetation. These provinces are frequently designated as Atlántica, Cerrado, Paranaense, and Yungas (Dominio Amazónico), and Chaco, Espinal, Monte, and Pampas (Dominio Chaqueño) (e.g., Cabrera, 1976; Cabrera & Willink, 1980). *Ruellia* species are found in all these floristic provinces, except in the dry Monte. The climate of these areas varies from hot and wet year-round, with over 2,000 mm rainfall, to warm and wet in summer and mild and dry in winter, with ca. 500 mm of rainfall especially during the summer months (from November to April).

Most of the species grow well in open and disturbed places, such as seasonally flooded areas or savannas with periodic fires, and are common in secondary growth. Even the ones that grow in the understory of forests are generally found in clearings and openings, roadcuts, and along stream or river banks. These characteristics together with their facultatively autogamous breeding system and mode of dispersal by animals (ectozoochory) make many species good colonizers and assure their success in long-distance dispersal events. This in some cases renders them important weeds in tropical and subtropical regions (e.g., *Ruellia ciliatiflora*).

Cultivation as ornamentals may have also helped to extend the natural range of some of the species, such as *Ruellia brevifolia*, which has become naturalized in many tropical places of the world (see Ezcurra, 1989).

## Economic Importance

Several species of *Ruellia* are cultivated mostly because of their showy flowers, sometimes in combination with attractive foliage. A few of the native ones from southern South America are frequently grown in warm regions all around the world, such as the red-flowered *Ruellia brevifolia* (generally known in horticulture as *R. graecizans*) and *Ruellia elegans* (syn.: *R. formosa*) (e.g., Everett, 1982). Other species of the area, such as *Ruellia angustiflora* and the blue-flowered *R. ciliatiflora* (generally reported as *R. lorentziana*), are not so common, and are cultivated more rarely (Dimitri, 1972; Ezcurra, 1989). Some of these subtropical species are probably hardier than their more tropical relatives and may adapt better to cooler regions of the world, hence they could be introduced in cultivation.

Some subtropical Acanthaceae native to north-

ern Argentina have been reported as having forage value (Burkart, 1943), especially in those areas with a seasonal climate with drier and colder periods where grasses are sometimes scarce. *Ruellia erythropus*, one of the most common and widespread species of *Ruellia* in southern South America, which is also found in southeastern Mexico, has been reported as good fodder (Burkart, 1943, erroneously as *Ruellia bahiensis*). This suggests it could be an important plant in the economy of those regions and should be investigated in relation to nutritional value.

## Taxonomic Treatment

**Ruellia** L., Sp. Pl. 634. 1753. TYPE: *R. tuberosa* L. (lectotype, selected by Britton & Brown (1913)).

*Stephanophysum* Pohl, Pl. Bras. Icon. Descr. 2: 83. 1831. TYPE: *Stephanophysum longifolium* Pohl (lectotype, selected by Bremekamp & Nannega Bremekamp (1948)).

*Dipteracanthus* Nees in Wallich, Pl. Asiat. Rar. 3: 75, 81. 1832. TYPE: *Dipteracanthus prostratus* Nees.

*Aphragmia* Nees in Lindl., Nat. Syst. Bot. ed. 2: 444. 1836. TYPE: *Aphragmia haenkei* Nees.

*Gymnacanthus* Nees in Lindl., Nat. Syst. Bot. ed. 2: 444. 1836, non Oersted 1854. TYPE: *Gymnacanthus petiolaris* Nees.

*Cryphiacanthus* Nees in Index Sem. Hort. Vratislav. 1841; Linnaea 16: 298. 1842. TYPE: *Cryphiacanthus barbadensis* Nees nom. illeg. (= *R. tuberosa* L.).

*Scordoxylum* Nees in Benth., Pl. Hartw.: 236. 1846. TYPE: *Scordoxylum hartwegianum* Nees.

*Sclerocalyx* Nees in Benth., Bot. Voy. Sulphur 145. 1846. TYPE: *Sclerocalyx mexicanus* Nees.

*Siphonacanthus* Nees in C. Martius, Fl. Bras. 9: 45. 1847. TYPE: *Siphonacanthus villosus* Nees.

*Eurychanes* Nees in C. Martius, Fl. Bras. 9: 52. 1847. TYPE: *Eurychanes verbasciformis* Nees ("verbascifolius").

*Stemonacanthus* Nees in C. Martius, Fl. Bras. 9: 53. 1847. TYPE: *Stemonacanthus salviaefolius* Nees (lectotype, selected by Leonard (1951–1958)).

*Arrhostoxylon* Nees in C. Martius, Fl. Bras. 9: 57. 1847. TYPE: *Arrhostoxylon glabrum* Nees (lectotype, selected by Bremekamp & Nannega Bremekamp (1948)).

*Penstemonacanthus* Nees in C. Martius, Fl. Bras. 9: 159. 1847. TYPE: *Penstemonacanthus modestus* Nees.

*Gymnacanthus* Oersted, Vidensk. Meddel. Dansk. Naturhist Foren. Kjobenhavn 1854: 126. 1854, not Nees, 1836. TYPE: *Gymnacanthus geminiflorus* (HBK) Oersted (= *Ruellia geminiflora* HBK).

*Blechum* Nees subgen. *Chiloblechum* Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1854: 169. 1854. TYPE: *Blechum mexicanum* Oersted (lectotype, selected here).

*Copioglossa* Miers, Proc. Roy. Hort. Soc. 3: 294. 1863. TYPE: *Copioglossa pilosa* Miers.

*Tremacanthus* S. Moore, J. Bot. 42: 33. 1904. TYPE: *Tremacanthus roberti* S. Moore.

*Salpingacanthus* S. Moore, J. Bot. 42: 107. 1904. TYPE: *Salpingacanthus nobilis* S. Moore.

*Ulleria* Bremek. Proc. Kon. Ned. Akad. Wetensch. Ser. C, 72, 14: 423. 1969. TYPE: *Ulleria geminiflora* (HBK) Bremek. (= *Ruellia geminiflora* HBK).

Perennial herbs, shrubs or subshrubs, erect to decumbent, ± pubescent. Leaves opposite, petiolate or subsessile, the blades entire, crenate or slightly dentate, with cystoliths. Flowers sessile or pedicellate, in axillary sessile dichasia or in pedunculate multiflowered cymes; the bracts and bracteoles generally small, not imbricate. Chasmogamous flowers medium or large, showy, blue, purple, or red, to mauve, lavander, pink, and white, rarely yellowish; cleistogamous flowers small and tubular. Calyx deeply cleft, the five segments linear or lanceolate, usually subequal, sometimes the posterior longer, rarely the lateral united to the anterior ones. Corolla straight or incurved, tubiform, funnelform or salverform, the basal portion of the tube narrow, abruptly or gradually dilated to a ± obconic or campanulate throat, sometimes anteriorly inflated or more rarely saccate, the limb generally spreading and oblique, sometimes erect, the five lobes ovate or rounded, contorted in bud, equal, sometimes the two posterior ± connate, forming a posterior lip. Stamens four, generally didynamous, included or exserted, the filaments inserted below the throat of the corolla, slightly dilated at the base, the anthers bithecous, oblong-sagittate, dorsifixed, the thecae parallel, equal, muticous. Pollen spheroidal, porate, coarsely reticulate. Disc inconspicuous; style slender, subulate, bilobate, the anterior lobe recurved, the posterior lobe generally reduced or obsolete; ovules 2–14 in each locule. Capsule clavate, obovate, oblong-linear or narrowly elliptic in contour, contracted and ± stipiform at the base, terete or somewhat compressed above. Seeds 4–28, compressed and flat, obliquely ovate or suborbicular, with appressed hairs that extend and turn mucilaginous when wet, subtended by retinacula ± acute.

## Key to the Species and Species Groups of *Ruellia* in Southern South America

1a. Corollas red ..... Group I. *Physiruellia*

2a. Flowers in long-pedunculate, cymose, multiflowered inflorescences subtended by the upper leaves; basal tube of the corolla frequently of the same length or shorter than the throat.

3a. Corolla lobes 0.5–1 cm diam.; calyx segments oblanceolate or spathulate.
4a. Erect herbs 30–50 cm tall ..... 1. *R. elegans*
4b. Scandent shrubs or subshrubs to 2 m tall ..... 2. *R. reitzii*
3b. Corolla lobes less than 0.5 cm diam.; calyx segments linear or oblong, acute or obtuse but not spathulate.
5a. Throat notably ventricose; basal tube less than 8 mm long ..... 3. *R. brevifolia*
5b. Throat not ventricose; basal tube more than 10 mm long.
6a. Young stems sharply quadrangular, with acute angles; Brazil, Paraguay, northern Uruguay, and northeastern Argentina ..... 4. *R. angustiflora*
6b. Stems obtusely quadrangular, rounded in the angles; Bolivia and northern Argentina ..... 5. *R. longipedunculata*
2b. Flowers solitary and sessile or shortly pedunculate in the axils of the upper leaves; basal tube of the corolla generally longer than the throat; Bolivia and northern Argentina ..... 6. *R. sanguinea*
1b. Corollas white, mauve, or blue.
7a. Flowers always in pedunculate, cymose, multiflowered inflorescences (subsessile and solitary only in some rosette plants) ..... Group II. *Ruellia*
8a. Caulescent herbs.
9a. Corollas mauve or blue, rarely white, with basal tube less than 2 cm long; calyx lobes less than 1 cm long.
10a. Leaves ± pubescent; flowers in cymes aggregated into a terminal, pyramidal thyrse ..... 7. *R. ciliatiflora*
10b. Leaves glabrous; flowers in lateral, axillary cymes ..... 8. *R. coerulea*
9b. Corollas white, with basal tube 2.5–5 cm long; calyx lobes 1.5 2 cm long ..... 9. *R. macrosolen*
8b. Acaulescent rosette plants.
11a. Corollas bluish, in lax, elongate pseudoracemes; pedicels puberulous or glabrous ..... 10. *R. hygrophila*
11b. Corollas white, generally subsessile and solitary; pedicels hirsute-tomentose ..... 11. *R. morongii*
7b. Flowers sessile, rarely pedunculate, solitary in the axils of the upper leaves, rarely in twos or threes.
12a. Bractlets present, and as long as or longer than the calyx segments.
13a. Stems sharply quadrangular ..... Group III. *Hygrophiloidei*
14a. Flowers more than 2 cm long, purple ..... 12. *R. epallocaulos*
14b. Flowers less than 2 cm long, white ..... 13. *R. kleinii*
13b. Stems obtusely quadrangular or terete ..... Group IV. *Dipteracanthus*
15a. Basal tube of the corolla shorter than the throat.
16a. Leaves tomentose with sessile glands intermingled with simple hairs ..... 14. *R. brachysiphon*
16b. Leaves with lax, spreading, shiny hairs, without glands ..... 15. *R. brevicaulis*
15b. Basal tube of the corolla the same length as or longer than the throat.
17a. Leaves and stems velutino-tomentose or velutino-hirsute ..... 16. *R. multifolia*
17b. Leaves and stems glabrous ..... 17. *R. solitaria*
12b. Bractlets obsolete or absent.
18a. Basal tube of the corolla shorter than the throat; placentas not separating from the capsule; seeds (2–)4 ..... Group V. *Ebracteolati*
19a. Leaves glabrous and coriaceous; nodes and calyx lobes glabrous; underground xylopodium rounded and tuberculate ..... 18. *R. bulbifera*
19b. Leaves ± pubescent and not coriaceous; nodes and calyx lobes generally white-tomentose; xylopodium not markedly rounded and tuberculate.
20a. Roots fibrous; leaves elliptic or ovate, sometimes lanceolate, 2–5 cm long, corolla 3–4 cm long ..... 19. *R. geminiflora*
20b. Roots, fleshy, fusiform; leaves lanceolate, 5–9 cm long; corolla 4–6 cm long ..... 20. *R. magniflora*
18b. Basal tube of the corolla the same length as the throat or longer. Placentas separating or not from the capsule; seeds 4–8.
21a. Basal tube of the corolla more than 6 cm long; placentas not separating from the capsule; seeds 6–8 ..... Group VI. *Salpingacanthus*
21. *R. nobilis*
21b. Basal tube of the corolla less than 5 cm long; placentas separating with the retinacula and seeds from the capsule, breaking the walls; seeds 4–6 ..... Group VII. *Chiloblechum*
22a. Leaves 2–5 cm long, the ones subtending the flowers subsessile and markedly ciliate; calyx segments unequally cleft, forming a three-lobed structure ..... 22. *R. erythropus*
22b. Leaves 1.5–2 cm long, the ones subtending the flowers glabrous or puberulous. Calyx segments 5 and subequally cleft ..... 23. *R. hypericoides*

## I. Group **Physiruellia**

*Ruellia* L. sect. *Physiruellia*, Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 311. 1895. *Ruellia* L. sect. *Physiruellia* Lindau ser. *Eglandulosae* Lindau, loc. cit.: 311. 1895. TYPE: *Ruellia acutangula* Nees (lectotype, selected here).

*Stephanophysum* Pohl, Pl. Bras. 2: 83. t. 155, 156. 1830 1831. TYPE: *Stephanophysum longifolium* Pohl (lectotype, selected by Bremekamp & Nannega Bremekamp (1948)).

*Scordoxylum* Nees in Benth., Pl. Hartw.: 236. 1846. TYPE: *Scordoxylum hartwegianum* Nees.

*Arrhostoxylon* Nees in C. Martius, Fl. Bras. 9: 57. 1847. TYPE: *Arrhostoxylon glabrum* Nees (lectotype, selected by Bremekamp & Nannega Bremekamp (1948)).

*Stemonacanthus* Nees in C. Martius, Fl. Bras. 9: 53. t. 54. 1847. TYPE: *Stemonacanthus salviaefolius* Nees (lectotype, selected by Leonard (1951–1958)).

Flowers pedicellate, borne in dichasial cymes subtended by the upper leaves, sometimes reduced to solitary flowers always pedicellate and bibracteolate. Capsules clavate, narrowly oblanceolate in contour, hollow the upper ⅔ of the total length, solid and stipitate in the base. Seeds 8–14.

Group *Physiruellia* is restricted to the New World and consists of numerous suffruticose plants that are frequent in the understory of tropical and subtropical forest. In southern South America they are important in floristic provinces of the Amazon region or dominion (see Cabrera & Willink, 1980). It is a large and very diversified assemblage which, on being studied in detail, may be divided into further gruops of closely allied species. Many of the species present handsome ornithophilous flowers, frequently red or pink.

**1. Ruellia elegans** Poiret, Encycl. Suppl. 4: 727. 1816. *Ruellia formosa* Andr. Bot. Repos. 10: tab. 610. 1810, non *Ruellia formosa* Humb. & Bonpl. 1805. *Arrhostoxylon formosum* (Andr.) Nees in C. Martius, Fl. Bras. 9: 62. 1847. *Arrhostoxylum elegans* (Poiret) Bremek. Verh. Nederl. Akad. Wet. (Tweede Sect.) 45(1): 12. 1948. TYPE: Illustrated in Andr. Bot. Repos. 10: tab. 610. 1810. Figure 6.

*Arrhostoxylon silvaccola* Nees var. *montanum* Nees in C. Martius, Fl. Bras. 9: 60. 1847. Syn. nov. SYNTYPES: Brazil. Minas Gerais: Mariana, *Langsdorf s.n.* (K), *Martinus s.n.* (M not seen, photo F 20524); *Sellow 104* (B destroyed), *263* (B destroyed; isosyntypes, K, P).

Erect suffruticose herb 30–50 cm tall, with few, sparsely branched, erect or decumbent stems, quadrangular and pubescent when young, glabrescent at maturity. Leaves on pilose petioles 0.5–3 cm long, the blade widely ovate, 4–9 cm long and 2–5 cm wide, obtuse and acuminate, widely cuneate on the base and somewhat decurrent on the petiole, the surface ± pilose when young, glabrescent at maturity, the margins ciliate. Flowers pedicellate, borne in long-pedunculate, few-flowered, lax, dichasial cymes, arising from the axils of the upper leaves; bracteoles narrowly oblong-spathulate or linear, less than 1 cm long and 2 mm wide, pubescent. Calyx ca. 1.5 cm long, the segments linear-spathulate, pubescent and glandular-ciliate. Corollas red, somewhat bilabiate, the basal tube 2–4 mm long, the throat curved, narrowly obconical, 2.5–3.5 cm long and 1 cm diam. at the orifice, the two posterior lobes erect, 1.5 cm long, united more than half their length, the three anterior spreading, ca. 1.5 cm diam. Stamens 3–4 cm long, subexserted under the posterior lobes, one pair somewhat shorter, anthers 3 mm long. Capsule elliptic-obovate, ca. 2 cm long and 5 mm thick, hollow nearly to the base, glabrous. Retinacula acute, 2 mm long. Seeds more than 12, flat, suborbicular, 2–3 mm wide, appressed-pubescent.

*Distribution.* Southeastern and central Brazil, from Minas Gerais to Paraná. It is found in disturbed, more or less open places, such as borders of Cerrado forest and mesophilous gallery forests. It flowers in spring and summer.

*Representative specimens.* BRAZIL. **Minas Gerais:** Estrada entre Araxá e Uberaba, km 381, em cerrado, 100 m.s.m., *Shepherd 7220* (MBM). **Paraná:** Mun. Cerro Azul, Cerro Azul, *Hatschbach 6401* (MBM, US).

*Ruellia elegans* is morphologically similar to some species of group *Ruellia* in the structure of the capsule and the herbaceous habit, but the calyx and corolla morphology place it close to *Ruellia sceptrum-marianum* (Vell. Conc.) Stearn, *R. acutangula* (Nees) Lindau, *R. silvaccola* (Nees) Lindau, and other related species of group *Physiruellia*. The similarities in vegetative and fruit characters to species of group *Ruellia* may just be a case of convergence within the evolution of group *Physiruellia*. It is a beautiful plant with large red flowers, sometimes cultivated as an ornamental. Human activities may have helped to extend its natural range.

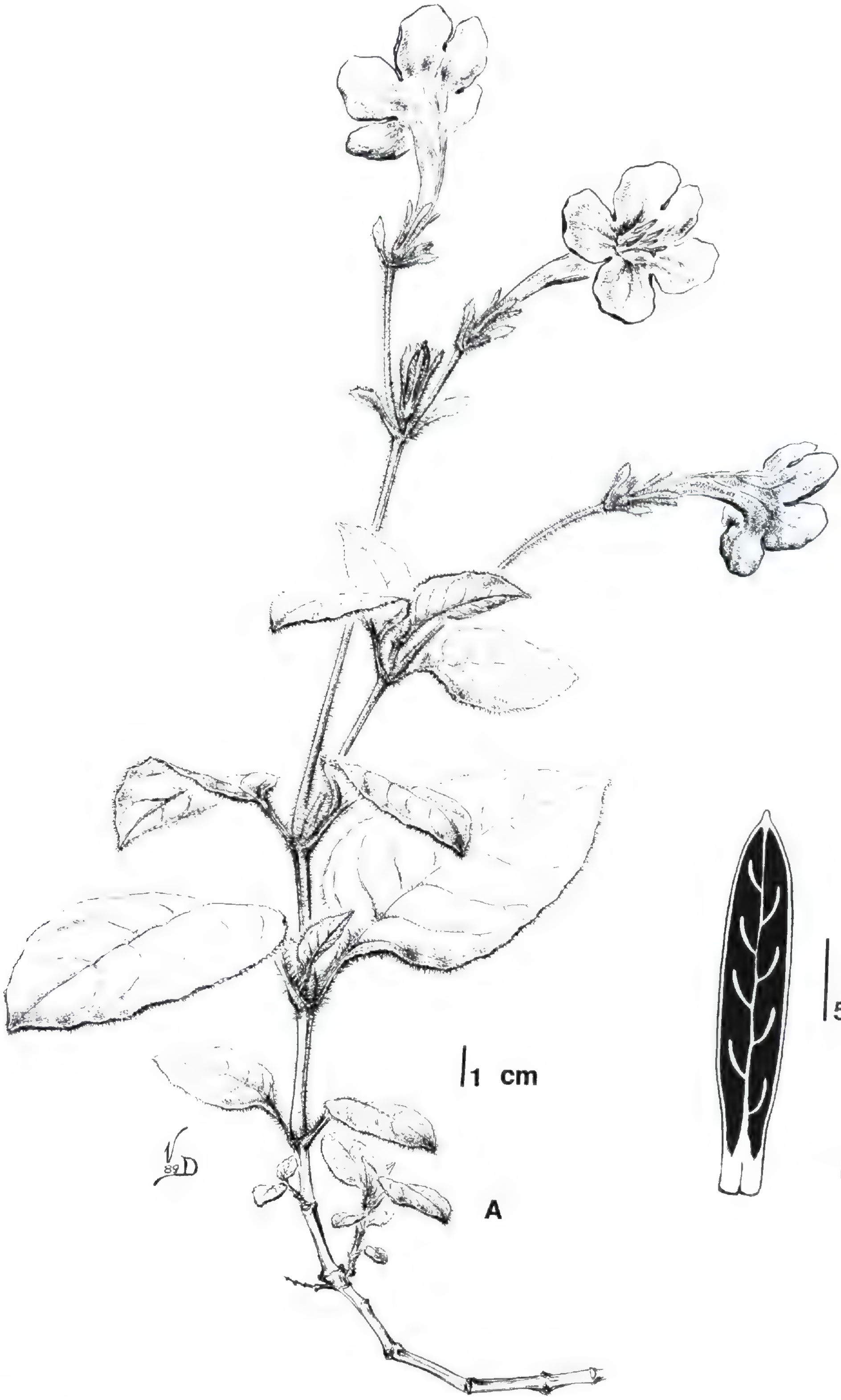


FIGURE 6. *Ruellia elegans* Poiret.—A. Flowering branch.—B. Immature capsule without seeds, schematic. (A, *Hatschbach 6401*; B, *Shepherd 7220*.)

**2. Ruellia reitzii** Wasshausen & Smith in Reitz, Fl. Illustr. Catarinense ACAN: 60. 1969. TYPE: Brazil. Santa Catarina: Luis Alves, Rio Canoas, 18 Jan. 1953, *Reitz 5154* (holotype, US).

Scandent or straggling shrub to 2 m tall, with sparsely branched stems, the younger portions markedly quadrangular, glabrous or pubescent, the older portions subterete and inflated over the nodes, becoming woody. Leaves on petioles 0.7–1.5 cm long, the blades ovate or elliptic, 3–7(–15) cm long and 1.5–3(–6) cm wide, acute or acuminate, cuneate at the base and somewhat decurrent on the petiole, irregularly and shallowly crenate, the surface glabrous to lightly velutino-puberulous, with trichomes mostly eglandular. Flowers pedicellate, in pedunculate cymes borne in the axils of the terminal leaves; peduncles 3–7 cm long; compound dichasia unevenly ramified (anisocladous), generally longer than the subtending leaves, frequently with supernumerary buds in the ramifications; bracteoles obovate, spathulate to oblanceolate, small, the lower ones generally foliaceous, more than 1 cm long. Calyx segments oblanceolate or spathulate, 12–14 mm long and 4–5 mm wide, rounded, puberulous. Corolla red, ca. 5 cm long, curved, the basal tube 1.5 cm long and 2 mm wide, opening into a cylindrical throat 1–2 cm long and 8–10 mm wide, the lobes semi-erect, rounded, 2 cm long and 1.5 cm wide, emarginate. Stamens exserted with anthers 4 mm long, laterally connate. Ovary pubescent; style exserted. Capsule unknown.

*Distribution.* Southern Brazil, in the state of Santa Catarina. In flower in January.

*Representative specimens.* BRAZIL. **Santa Catarina:** Braço Serafim, Margem de cascata, *Reitz C 2009* (HBR, US).

*Ruellia reitzii* is characterized by the large red flowers in multiflowered dichasial cymes and the spathulate or oblanceolate, pubescent calyx lobes. In these characters it shows close affinities with the group of *Ruellia acutangula* (Nees) Lindau, *R. sceptrum-marianum* (Vell. Conc.) Stearn, and related species of central and southeastern Brazil. *Ruellia reitzii* occurs more to the south and differs from these species principally by the weaker or scandent habit.

**3. Ruellia brevifolia** (Pohl) Ezcurra, Darwiniana 29: 278. 1989. *Stephanophysum brevifolium* Pohl, Pl. Bras. Icon. Descr. 2: 84, tab. 155. 1831. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Schott s.n.* (holotype, W not seen, photo SI). Figure 7.

*Ruellia ventricosa* HBK, Nov. Gen. Sp. 2: 241. 1817, not Poiret, 1804. *Stephanophysum ventricosum* (HBK) Nees in DC., Prodr. 11: 203. 1847. TYPE: Peru. "Prov. Jaen de Bracamoros, Chamayae prope Chavico," *Humboldt & Bonpland s.n.* (holotype, B destroyed, photo F 18410, isotype, P). Syn. nov.

*Stephanophysum longifolium* Pohl, Pl. Bras. Icon. Descr. 2: 85, tab. 156. 1831. *Ruellia longifolia* (Pohl) Griseb., Abh. Koenigl. Ges. Wiss. Goettingen 24: 260. 1879, not Richard, 1782. *Ruellia graecizans* Backer, Brittonia 3: 85, 87. 1938. TYPE: Brazil. Without locality: *Pohl s.n.* (syntype, W not seen, photo SI).

*Echinacanthus dichotomus* Kuntze, Revis. Gen. Pl. 2: 489. 1891, not *Ruellia dichotoma* Sessé & Moç., 1889. TYPE: Indonesia. Java: Bogor, Buitenzorg, *Kuntze*, 1875 (holotype, NY).

*Ruellia serratitheca* Rusby, Mem. New York Bot. Gard. 7: 362. 1927. TYPE: Bolivia. Without departamento: Canamina, 4,500 ft., 28 July 1921, *Rusby 363* (holotype, NY).

*Stephanophysum macrandrum* Bremek., Proc. Kon. Ned. Akad. Wetensch. Ser. C. 72, 4: 424. 1969. TYPE: Bolivia. Without depto.: Bartolo, 5,000 ft., 24 Sep. 1949, *Brooke 5681* (holotype, U). Syn. nov.

Suffruticose herb or subshrub to 1 m tall, with numerous erect stems, sparsely branched, obtusely subquadrangular when young, glabrous. Leaves on petioles 1–5 cm long, the blades ovate, 4–15 cm long and 1.5–8 cm wide, acuminate at the apex, cuneate at the base, entire or shallowly crenate, the surface generally glabrous, sometimes pubescent. Flowers pedicellate, borne in axillary, lax, long-pedunculate, multiflowered cymes of compound dichasia; supernumerary buds frequent in the ramifications. Bracteoles ovate or lanceolate, foliaceous, bigger than the calyx lobes. Calyx 5–10 mm long, the segments linear and acute, less than 1 mm wide, puberulous. Corollas curved, scarlet, the basal tube 0.5–1 cm long, opening into an anteriorly inflated, ventricose throat 1–1.5 cm long and 0.5–1 cm wide, narrower toward the orifice, the lobes suberect, small, rounded, 2–3 mm long, retuse. Stamens subexserted with filaments ca. 9 mm long, and anthers 3 mm long, laterally connate, basally apiculate. Ovary puberulous; style exserted. Capsule clavate, 1–1.5 cm long and 3 mm thick, broadest above the middle, solid-stipitate to 3 mm high, glabrous. Seeds 8–12, suborbicular, 2 mm diam., with hygroscopic-viscid pilose margins; retinacula 2 mm long.

*Distribution.* Tropical and subtropical South America, from Colombia, Ecuador, Peru, and Bolivia to southern Brazil, Paraguay, and northern Argentina. It is found in the understory of open places of the forest, such as clearings, borders of roads, and water courses, from sea level to 1,500 m altitude. It prefers disturbed, humid soil; it flow-

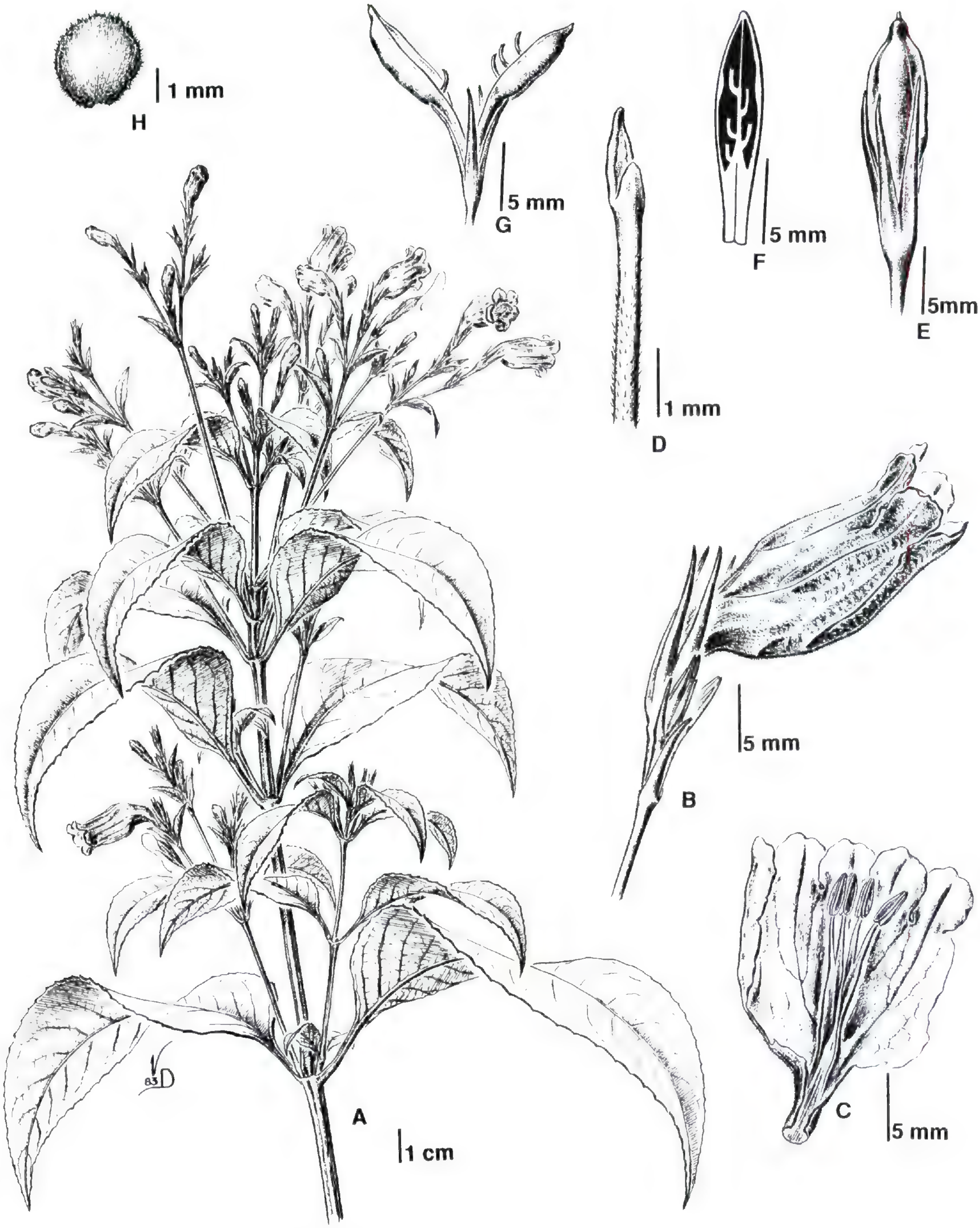


FIGURE 7. *Ruellia brevifolia* (Pohl) Ezcurra.—A. Flowering branch.—B. Flower.—C. Open corolla.—D. Stylar apex.—E. Capsule.—F. Open capsule without seeds, schematic.—G. Dehiscent capsule.—H. Seed. (A–E, G, H, *Cabrera 28048*. F, *Zuloaga 1629*.)

ers in autumn and winter, from March to September.

*Representative specimens.* ARGENTINA. **Jujuy:** Yuto, El Bananal, *Cabrera 28048, 33941* (SI), *Fabris 4541, 5045* (LP); Unión del Río Pantanoso y el Piedras, *Iudica & Ramadori 367* (SI); Arroyo Zanjón Seco, *Zuloaga 2501* (SI); Campamento Caimancito de Yacimientos Petrolíferos Fiscales, *Zuloaga 2534* (SI). **Misiones:** Cataratas del Iguazú, *Schulz 16192* (US). **Salta:** Río Pescado, *Borsini 580* (LIL); Caraparí, *Bridarolli 3258, 3261* (LP); Agua Blanca, *Cabrera 26534* (SI); Urundel,

Arroyo El Diablo, *Capurro 238* (BA); Pocitos, *Krapovickas 19415* (CTES); Vado Hondo, *Legname & Cuezzo 7045* (LIL, LP); Río Piedras, *Rodriguez 62* (BA, LP, SI); Río Tartagal, *Schreiter 3367* (LIL, SI, US), *10862* (LIL, NY, SI), *Venturi 10758* (SI); Camino a Finca La Ronda, Río Santa María a 15 km de Orán, *Zuloaga 1629* (SI); Camino de Ballivián a Río Seco, *Zuloaga 2685* (SI). **Tucumán:** Capital, Río Salí frente al Boulevard Sarmiento, *Venturi 3821* (BA, US), *3957* (SI, US). **Entre Ríos:** Concordia, *Spegazzini*, VI-1949 (BAB). BRAZIL. **Paraná:** Iguaçu Falls, *Davis & Shepherd 60927* (MBM); Morretes, *Dusén 14022* (GH, MO, NY, SI, US), *Hatschbach 116* (MBM); Cerro Azul, *Hatschbach 2326* (MBM, US); Antonina, estrada Cacatu - Serra Negra, *Hatschbach 12800* (MBM); Rio Cachoeira, *Hatschbach 34410* (MBM, US); Mun. Jacarezinho, Riacho da Fartura, *Kummrow 525* (MBM); Mun. Terra Boa, Rio Ivaí, *Lindeman 626* (MBM, US). **Rio Grande do Sul:** São Leopoldo, Spigelbey, *Schultz 397* (ICN). **Santa Catarina:** Ibirama, capoeira, *Gevieski 58* (HBR, RB); Brusque, Azambuja, *Klein 2775* (HBR, US); Florianopolis, Ilha de Santa Catarina, morro costa da lagoa, *Klein 7431* (HBR, R, US); Porto Belo, Caixa d'Aço, *Smith 12310* (HBR, NY, RB, US). PARAGUAY. **Alto Paraná:** Hernandarias, *Bertoni 4373* (LIL); Ruta 7, Km A-252, *Boelcke 13485* (BAB, CTES); 60 km al N de Hernandarias, *Fernández Casas 7587* (G, MO); 35 km N of Hernandarias, *Hahn 925* (MO, US); Ruta 2, km 252, *Krapovickas & Cristóbal 13407* (SI, US); Itabo, barrage d'Itaipu, 70 km N de Pto. Stroessner, *Billiet & Jadin 3478* (BM, NY, MO). **Canendiyú:** Yerbales, Sierra de Maracayu, *Hassler 4508* (BM, MO, P).

*Ruellia brevifolia* is characterized by the small scarlet, ventricose flowers with inflated corollas in multiflowered cymes. It is one of the most widely distributed species in South America, ranging from Colombia to northern Argentina. It shows a large amount of variation over its area, sometimes presenting pubescent leaves or larger-flowered populations. It is used as an ornamental in tropical regions all over the world, where it often becomes naturalized (Ariza Espinar, 1983; Backer & Bakhuizen van den Brink, 1965; Barker, 1986). Its cultivation in South America may have helped to extend its natural range through garden escapes and establishment in new areas (Ezcurra, 1989). *Ruellia amoena* Nees and *Cyrthacanthus corymbosus* Martius ex Nees are nomina nuda that have been used for this species in herbaria (Nees, 1847b).

4. **Ruellia angustiflora** (Nees) Lindau ex Rambo, Iheringia, Bot. 12: 23. 1964. *Stephanophysum angustiflorum* Nees in C. Martius, Fl. Bras. 7: 51. 1847. SYNTYPES: Brazil. Rio Grande do Sul: Porto Alegre, *Isabelle s.n.* (K); *Sellow s.n.* (B destroyed, photo F 5909; isosyntype, K); *Joannes de S. Barbara s.n.* (not seen); *Tweedie s.n.* (K). Figure 8.

Erect or somewhat scandent shrub to 2 m tall, with sparsely branched stems, the younger portions sharply quadrangular, glabrous, the older portions subterete and inflated over the nodes, becoming woody. Leaves on petioles 0.3–1.5(–4) cm long, the blades ovate or elliptic, 3–10(–15) cm long and 1.5–4(–6) cm wide, acute or acuminate, cuneate at the base and somewhat decurrent on the petiole, irregularly and shallowly crenate, the surface glabrous to lightly velutino-puberulous, with trichomes mostly eglandular. Flowers pedicellate, in pedunculate cymes borne alternatively on one of each pair (rarely on both) of the terminal leaves; peduncles 3–7 mm long; compound dichasia unevenly ramified (anisocladous), generally longer than the subtending leaves, frequently with supernumerary buds in the ramifications; bracteoles obovate to oblanceolate, small, the lower ones generally foliaceous, more than 1 cm long. Calyx segments linear-lanceolate, 4–12 mm long and 1–2 mm wide, acute, puberulous. Corolla red, 3–4(–6) cm long, angled, the basal tube 1–2 cm long, opening into a cylindrical throat 1–2 cm long and 8 mm wide, the lobes semi-erect, rounded, 5 mm long, emarginate. Stamens subexserted with filaments 1–1.5 cm long, and anthers 4 mm long, laterally connate, obtuse, and with glandular connective. Ovary glabrous; style exserted. Capsule clavate, 1.5–2 cm long and 4 mm thick, glabrous, broadest above the middle, the base solid to 3–5 mm high. Seeds 8–12, dark brown, 2 mm diam., with pilose margins, hygroscopic-viscid when wet; retinacula 2 mm long.

*Vernacular names.* "Flor de fogo," in Santa Catarina, Brazil (Wasshausen & Smith, 1969).

*Distribution.* Southern Brazil, northern Uruguay, eastern Paraguay, and northeastern Argentina, in the hygrophilous subtropical forests of the basins of the Rivers Paraná and Uruguay (Paranaense phytogeographical province). It is found in humid places, such as borders of streams, margins of rivers, and near waterfalls, in disturbed, open and sunny locations of the forest. It flowers in winter, spring, and summer, especially from July to February.

*Representative specimens.* ARGENTINA. **Corrientes:** Depto. San Martín, Tres Cerros, *Cabrera 27695, 28152* (SI); Depto. Ituzaingó, Rapidos de Apipé, *Cabrera 28969* (SI); San Cosme, *Cristóbal 191* (LIL); Paso de la Patria, *Cuezzo 11297* (LIL); Depto. San Martín, Colonia Caimán, *Ibarrola 4203* (LIL); Depto. Santo Tomé, Arroyo Chirimay, *Krapovickas 21097, 26163* (CTES, US); General Paz, 12 km de Ita Ibaté, costa Río Paraná, *Mroginski 674* (CTES, US); Depto. Mburucuyá, Estancia Santa Teresa, *Pedersen 1305* (LP, US); Berón de Astrada, *Ruiz-*

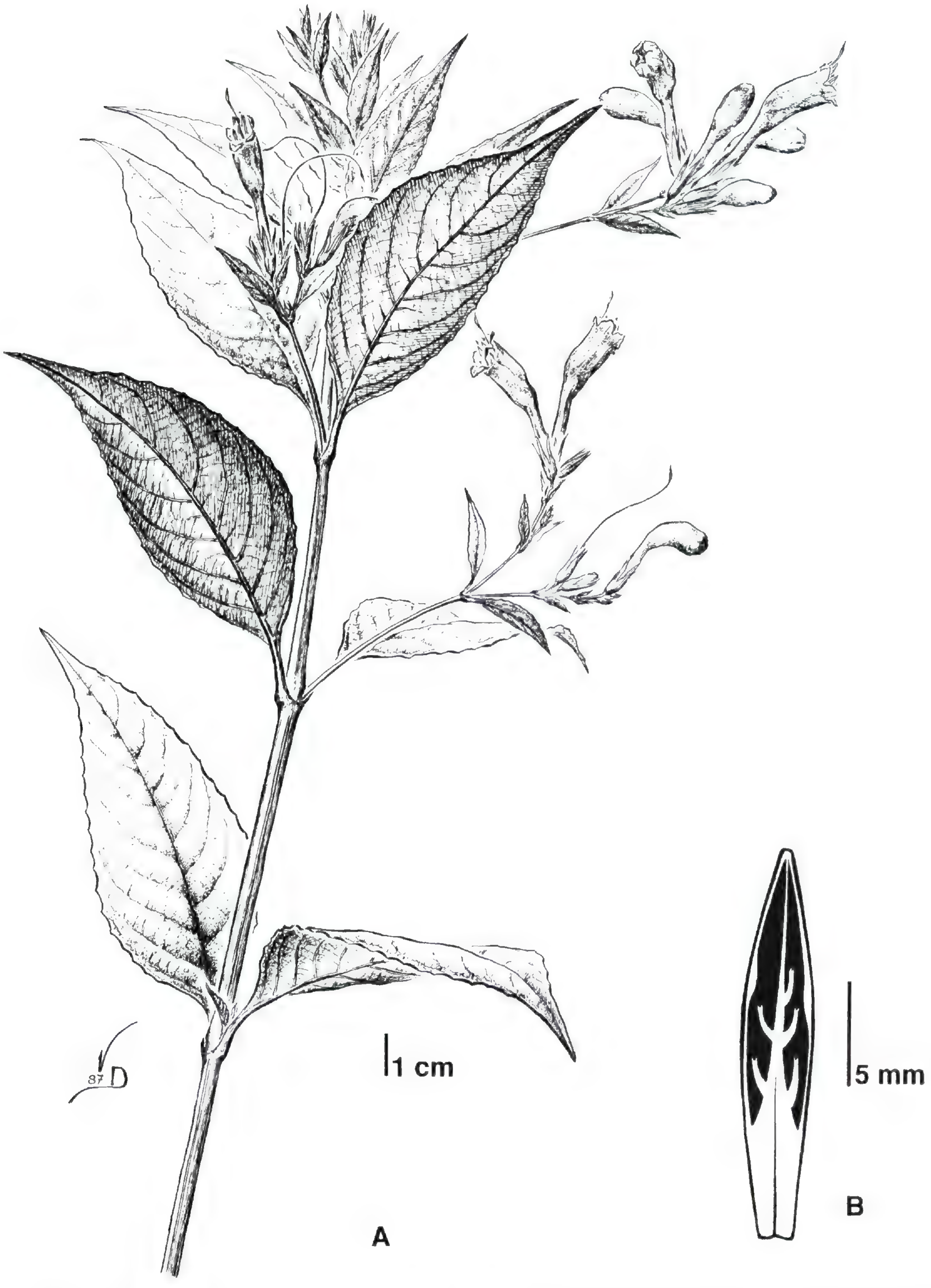


FIGURE 8. *Ruellia angustiflora* (Nees) Lindau ex Rambo.—A. Flowering branch.—B. Open capsule without seeds, schematic. (A, *Montes 15429*; B, *Cabrera 28969*.)

*Huidobro 2249* (NY, SI); Depto. Mercedes, Frente a Carlos Pellegrini, orilla laguna Iberá, *Schinini 7370* (CTES, US); Depto. Saladas, Pago de Los Deseos, *Schwarz 8969* (LIL); Depto. Concepción, 11 km NW de Santa Rosa, *Tressens 874* (CTES). **Entre Ríos:** Federación, *Martinez Crovetto y Piccinini 4694* (BAB, CTES, US). **Formosa:** Depto. Pilcomayo, Clorinda, *Cezzanni s.n.* (LP). **Misiones:** Depto. Iguazú, Cataratas, *Cabrera 184* (LP); Depto. Oberá, Oberá, *Cabrera 356* (LP); Depto. San Pedro, San Pedro, *Cabrera 28825* (SI); Depto. Apóstoles, San José, Escuela Agrotécnica Pascual Gentilini, *Cabrera 28483, 29260* (SI); Depto. Eldorado, Ruta 12, Arroyo Piray Guazú, *Crisci 269* (LP); Depto. General Belgrano, Bernardo de Irigoyen, *Hunziker 940* (SI); Depto. San Ignacio, Teyucuaré, 6 km de San Ignacio, *Krapovickas 2327* (LP); Depto. Leandro Alem, Cerro Azul, *Krapovickas & Cristóbal 15939* (BA, CTES, LP, NY, RB, US); Depto. San Javier, San Javier, *Krapovickas & Cristóbal* 28892 (SI); Depto. San Pedro, Laharrague, *Montes 15429* (SI). BRAZIL. **Mato Grosso do Sul:** Mun. Rio Brilhante, Fazenda Bela Vista, *Hatschbach 26079* (MBM, NY); Mun. Anastacio, Rio Aquidauana, *Hatschbach 24605* (MBM, US). **Paraná:** Mun. Tibagi, Fazenda Monte Alegre, *Hatschbach 2852* (MBM, RB), *7141* (MBM, US); Foz do Iguaçu, Cataratas, *Hatschbach 3900* (MBM); Mun. Cianorte, Fazenda Lagoa, *Hatschbach 16953* (MBM, US); Tapejara, *Hatschbach 17003* (MBM, US); Rio Branco do Sul, Ribeirinha, *Hatschbach 18079* (MBM, US); Porecatu, *Hatschbach 23475* (MBM, NY), *23485* (MBM, US); Matelandia, Santa Lucia, *Hatschbach 34526* (MBM, US). **Rio Grande do Sul:** 13 km S de Cruz Alta, *Krapovickas & Vanni 37067* (CTES, US); 13 km SE de Santa Rosa, *Lindeman 8962* (CTES, ICN); Porto Alegre, Tristeza, *Palacios & Cuezzo 500* (LIL); Cacapava do Sul, *Palacios & Cuezzo 1410* (LIL); 13 km de Carazinho a Sta. Barbara, *Quarín 1153* (CTES); Sta. Clara prope Lajeado, *Rambo 6516* (PACA); Jari prope Tupanciretan, *Rambo 9382* (PACA); Prope São Leopoldo, *Rambo 29483, 38859, 42095, 42635* (all LIL), *43937* (LIL, US), *44112* (LIL); Porto Alegre, *Rambo 26628* (US), *37803* (LIL); Prope Novo Hamburgo, *Rambo 42894* (LIL); Pareci Velho, *Rambo 43839* (LIL, US); Mato Leitao prope Venancio Aires, *Rambo 49489* (LIL); Itapiranga ad flumen Uruguay, *Rambo 53675* (PACA); Pelotas, *Sacco 1006* (PACA). **Santa Catarina:** Itapiranga, Tunas, *Klein 5149* (HBR); Chapeco, Capoeira, 300 m, *Klein 5310, 5602* (HBR, US); São Domingo, Coxilha Seca, Marata, *Klein 7784* (HBR, US); Lajes, Passo do Socorro, 800 m, *Reitz 6555* (HBR, RB, US); Capinzal, orla da mata, 500 m, *Reitz 16238* (HBR, US); Abelardo Luz, beira do rio, 950 m, *Reitz & Klein 16616* (HBR, US); Ibirama, ao longo do Rio Itajaí, *Smith, Klein & Gevieski 7612* (HBR, US); 9 km W de Campo Ere, 900–1,000 m, *Smith & Klein 11543* (HBR, NY, RB, US); Dionisio Cerqueira, 41 km ao S, *Smith & Klein 11710* (HBR, RB, US); Riqueza, *Smith & Klein 13128* (HBR, R, US). PARAGUAY. **Amambay:** Zwischen Río Apa und Río Aquidabán, *Fiebrig 4190* (BM, GH, K); Cursus superioris fluminis Apa, *Hassler 8089, 8089a* (BM, G, K, MO, NY, P); Pedro Juan Caballero, *Mizoguchi 462* (NY); Sierra de Amambay, Estrella, *Rojas 10153* (G); Parque Nacional Cerro Corá, vic. Cerro Muralla, *Solomon 6804* (G, MO, NY); Parque Nacional Cerro Corá, margen del Río Aquidabán, *Zardini 4207* (MO). **Alto Paraná:** Santa Teresa, *Bertoni 1690, 4280, 4419* (all LIL); in regione fluminis Alto Paraná, *Fiebrig 5370* (BM, G, GH, K); Ruta 2, km A 252, *Krapovickas & Cristóbal 13409* (CTES); Puerto Stroessner, Centre Forestier, *Stutz 166, 196, 325* (all NY). **Caaguazú:** Parque Guayaki, *Schulz 16203* (BAB, CTES, SI). **Caazapá:** Tavai, Propiedad Familia Bogado, *Basualdo 1933* (MO), *Ortiz 957* (G). **Canendiyú:** Yerbales, Sierra de Maracayú, *Hassler 4127* (BM, GH, MO), *4319* (BM, P). **Central:** Lacus Ypacaray, *Hassler 11744* (BM, GH, K, MO, NY); Yaguarón, Cerro Corá, *Krapovickas 12327* (CTES). **Cordillera:** Cordillera de Altos, *Fiebrig 104* (BM, G, GH, K); Valenzuela, Mboraya-guazu-ty, *Sparre & Vervoorst 1310* (LIL); Cerro Zanja Jhú, 1 km E of road from Route 1 to Atyra, 3 km from Atyra, *Zardini 5075, 6237* (MO). **Guairá:** Villa Rica, *Balansa 2457a* (P); Cordillera de Villa Rica, *Hassler 8824* (BM, G, GH, NY, P); Road Melgarejo-Antena, 6 km S of Melgarejo, *Zardini 11188* (MO). **Itapuá:** Arroyo San Rafael, Ruta 1, 15 km SE de General Delgado, *Arbo 2023* (CTES); Encarnación, alrededores, *Bertoni 5566* (LIL); El Tirol, pequeña reserva tras el hotel, *Brunner 868* (MO). **Misiones:** Estancia La Soledad, *Pedersen 14390* (GH, SI). **Paraguarí:** Paraguarí, *Balansa 2457* (K, P), *Fiebrig 906* (G, GH, K); Cerro Acahy, *Billiet & Jadin 3003* (BM); Entre Carapaguá y Acahy, bosque próximo a Riachuelo, *Fernández Casas 3518* (NY); Base del Cerro Yaguarón, *Schinini 4194* (CTES, G, SI); Compañía Costa II, Cerro Palacios, *Zardini 3100* (G, MO), *5621, 6424, 6430, 6490* (all MO); Cerro Mbatoví, *Zardini 4467* (MO); Macizo Acahay, forest on E peak, *Zardini 5271, 5691* (MO). **San Pedro:** Tapiraguay, *Hassler 4127, 4318, 4319* (all K, P, NY). URUGUAY: **Artigas:** San Gregorio, Riusa, *Del Puerto 2053* (MVFA). **Rivera:** Ruta 30, Subida de Pena, Sierra de la Aurora, *Rosengurtt B-7136* (MVFA).

*Ruellia angustiflora* is characterized by the markedly quadrangular stems and the bright red tubular flowers in multiflowered axillary cymes. It is frequent in the understory of gallery forests of southern Brazil, eastern Paraguay, northeastern Argentina, and northern Uruguay, and had been erroneously identified by many authors (e.g., Lindau, 1894; Wasshausen & Smith, 1969; Dawson, 1979) as *Ruellia sanguinea*, a species common in southern Bolivia and northern Argentina (see Ezcurra, 1989). It is often cultivated because of its handsome, red flowers and easy propagation. The isolated localities of the southernmost portion of its range (e.g., Entre Ríos, Federación) are probably the product of garden escapes.

5. **Ruellia longipedunculata** Lindau, Bull. Herb. Boissier 3: 365. 1895. TYPE: Bolivia. Santa Cruz: Santa Cruz, 2,600–1,000 m, *Kuntze*, May 1892 (holotype, B destroyed, photo F 18213; isotypes, NY, US). Figure 9.

*Stephanophysum brookeae* Bremek., Proc. Kon. Ned. Akad. Wetensch. Ser. C. 72, 4: 424. 1969. TYPE: Bolivia. Santa Cruz: Camiri, on Río Parapeti refinery and commencement of the pipeline, 2,500 ft., 3 Sep. 1949, *Brooke 5577* (holotype, BM; isotype, NY). Syn. nov.

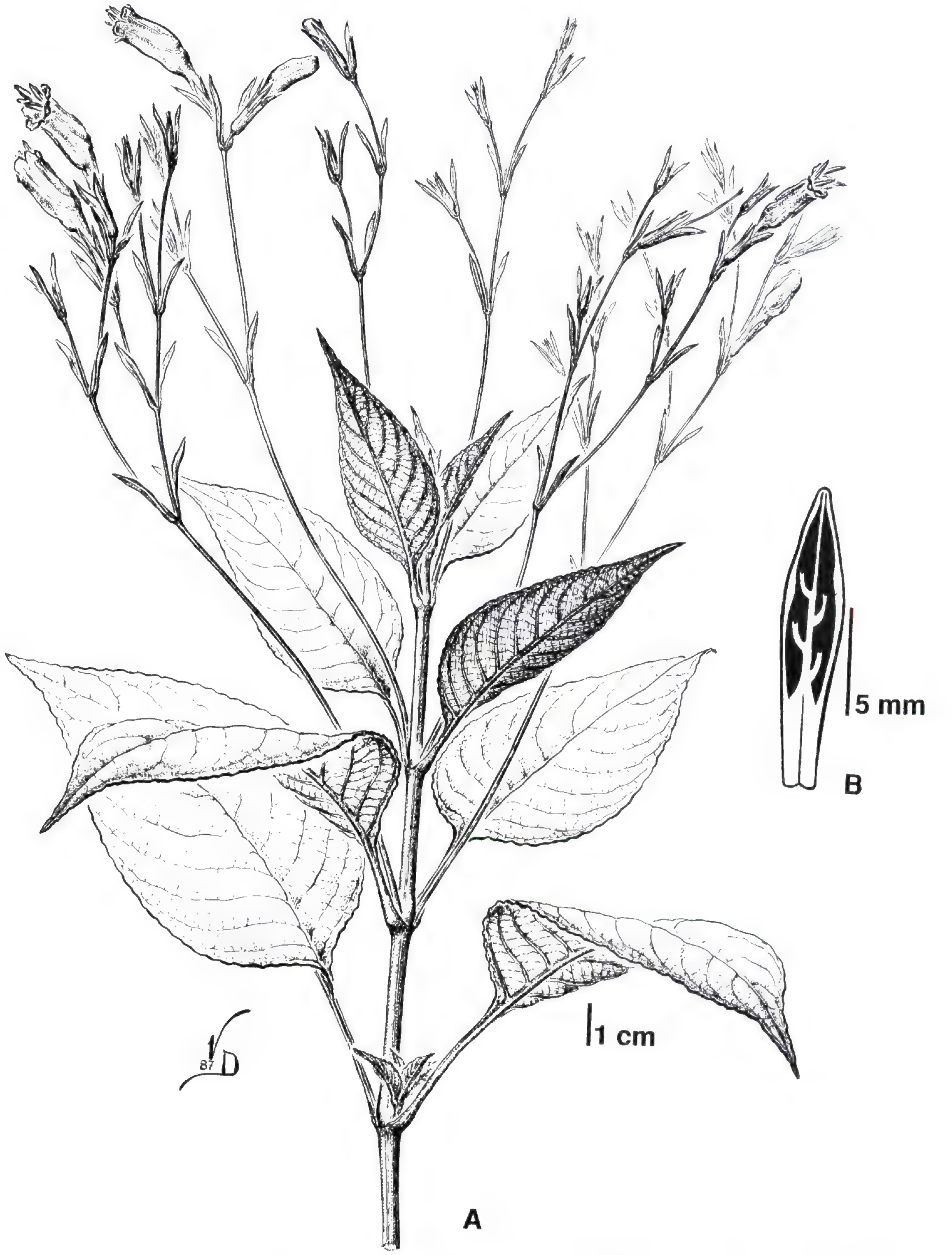


FIGURE 9. *Ruellia longipedunculata* Lindau. — A, Flowering branch. — B. Open capsule without seeds, schematic. (A, *Cabrera 26526*; B, *Cabrera 32782*.)

Stout suffruticose herb to 2 m high, the stems ascending, obtusely quadrangular, slightly hirsute-pilose when young, glabrescent at maturity. Leaves on petioles 0.5–2.5(–4) cm long, the blades ovate, 5–10(–15) cm long and 2–6(–8) cm wide, acuminate, obtuse or rounded at the base, irregularly and very shallowly crenate or dentate, the surface glabrous to lightly puberulous. Flowers pedicellate, in dichasia forming lax, long-pedunculate cymes, borne on both pairs of the terminal leaves, generally longer than the subtending leaves, frequently with supernumerary buds in the ramifications; bracteoles spathulate to oblanceolate, approximately 1.5 cm long and 1 mm wide, the lower ones generally larger and foliaceous. Calyx ca. 2 cm long, the segments oblong-lanceolate, 12–15 mm long and 2–3 mm wide, acute, glabrous, the superior somewhat larger. Corolla red, 2.5–3 cm long, the basal tube ca. 1.3 cm long, opening into a subcylindrical throat 1.5 cm long and 4–5 mm wide, the lobes semi-erect, rounded, 3–4 mm long. Stamens subexserted with filaments 13–15 mm long, and anthers 4 mm long. Ovary puberulous; style exserted. Capsule clavate, 1.5 cm long and 3 mm thick, glabrous, broadest above the middle, the base solid to 5 mm high. Seeds 6–8, dark brown, 2 mm diam., with pilose margins, hygroscopic-viscid when wetted; retinacula 2 mm long.

*Distribution.* Southeastern Bolivia and northern Argentina, in low mountain forests of the Yungas phytogeographical province, near transition to the more xerophilous Chaco forest. It is found in the underwood, in openings and borders of paths, rivers, and streams. It flowers in spring, from September to December, and could be used as an ornamental.

*Representative specimens.* ARGENTINA. **Jujuy:** Camino a Valle Grande, *Cabrera 27816* (LP, SI); Serranía de Calilegua, El Cebilar, *Fabris 4436* (LP); Mesada de Las Colmenas, *Iudica & Ramadori 5* (SI); Camino de la toma del Río Zora a Cafetales, *Zuloaga 2903* (SI). **Salta:** Agua Blanca, *Cabrera 26526* (LP, SI); Depto. Chicoana, Los Laureles, *Cabrera 32782* (SI); Quebrada de Escoipe, *Zardini 1205* (LP); Ruta Nac. 34, Dique Itiyuro, *Zuloaga 2728* (SI).

*Ruellia longipedunculata* is characterized by the long, somewhat pendulous, multiflowered inflorescences, the wide calyx lobes, and the narrow red corollas. Specimens that are morphologically intermediate with *Ruellia brevifolia* in these characters suggest natural hybridization in areas where these species are sympatric (Ezcurra, 1989).

**5a. Ruellia longipedunculata** Lindau × **Ruellia brevifolia** (Pohl) Ezcurra.

Plants similar to *Ruellia longipedunculata*, but differing by the shorter and narrower calyx lobes and the shorter and somewhat inflated corolla throats.

*Representative specimens.* ARGENTINA. **Salta:** camino a la finca Yakúlica, aprox. 5 km del Puente Agua Blanca, *Cuezzo 11718* (LIL, pro parte); Ruta Nac. 34, Dique Itiyuro, *Zuloaga 2730* (SI).

These specimens, which are morphologically intermediate between *Ruellia longipedunculata* and *R. brevifolia*, also show reduced pollen fertility, which suggests hybridization (Ezcurra, 1989).

**6. Ruellia sanguinea** Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 260. 1879. TYPE: Argentina. Salta: Orán, prope San Andrés, Rio Seco bei San Andrés, 17–24 Sep. 1873, *Lorentz & Hieronymus 269* (holotype, GOET not seen, photo SI, US; isotype, B destroyed, photo F 18209). Figure 10.

*Ruellia kuntzei* Lindau, Bull. Herb. Boissier 3: 365. 1895. *Arrhostoxylum kuntzei* (Lindau) Bremek., Proc. Kon. Ned. Akad. Wetensch. Ser. C, 72, 4: 424. 1969. TYPE: Bolivia. Without locality: 2,000 m, *Kuntze*, Apr. 1892 (holotype, B destroyed, photo F 18209; isotype, NY).

Suffruticose subshrub to 1.5 m high, the stems ascending, markedly quadrangular, slightly pubescent when young, terete and glabrescent at maturity. Leaves on petioles 2–8 cm long, the blades ovate, 6–16 cm long and 4–8 cm wide, acuminate and cuspidate, obtuse and somewhat decurrent on the petiole at the base, smooth or irregularly and very shallowly crenate or dentate, the surface glabrous to slightly puberulous. Flowers subsessile or very shortly pedunculate, solitary in the axils of reduced upper leaves, frequently with supernumerary buds in the axils of the subtending leaves; bracteoles narrowly oblanceolate or lanceolate, approximately 5 mm long and 1 mm wide. Calyx 8–10 mm long, the segments linear, 5–7 mm long and 1 mm wide, acute, ciliate. Corolla red, 3–5 cm long, puberulous, the basal tube thin and curved, 1.5–3 cm long, opening into an abconic throat 1.5–2 cm long and 5–8 mm wide, the lobes semi-erect, rounded, 3–5 mm long, somewhat retuse. Stamens subexserted with filaments 5–7 mm long, and anthers 3.5 mm long. Ovary puberulous; style exserted. Capsule clavate, 1.5 cm long and 3–4 mm thick, glabrous, broadest above the middle, the base solid to 5 mm high. Seeds 8–10, dark brown, 2–3 mm diam., with pilose margins, hygroscopic-viscid when wet; retinacula 2 mm long.

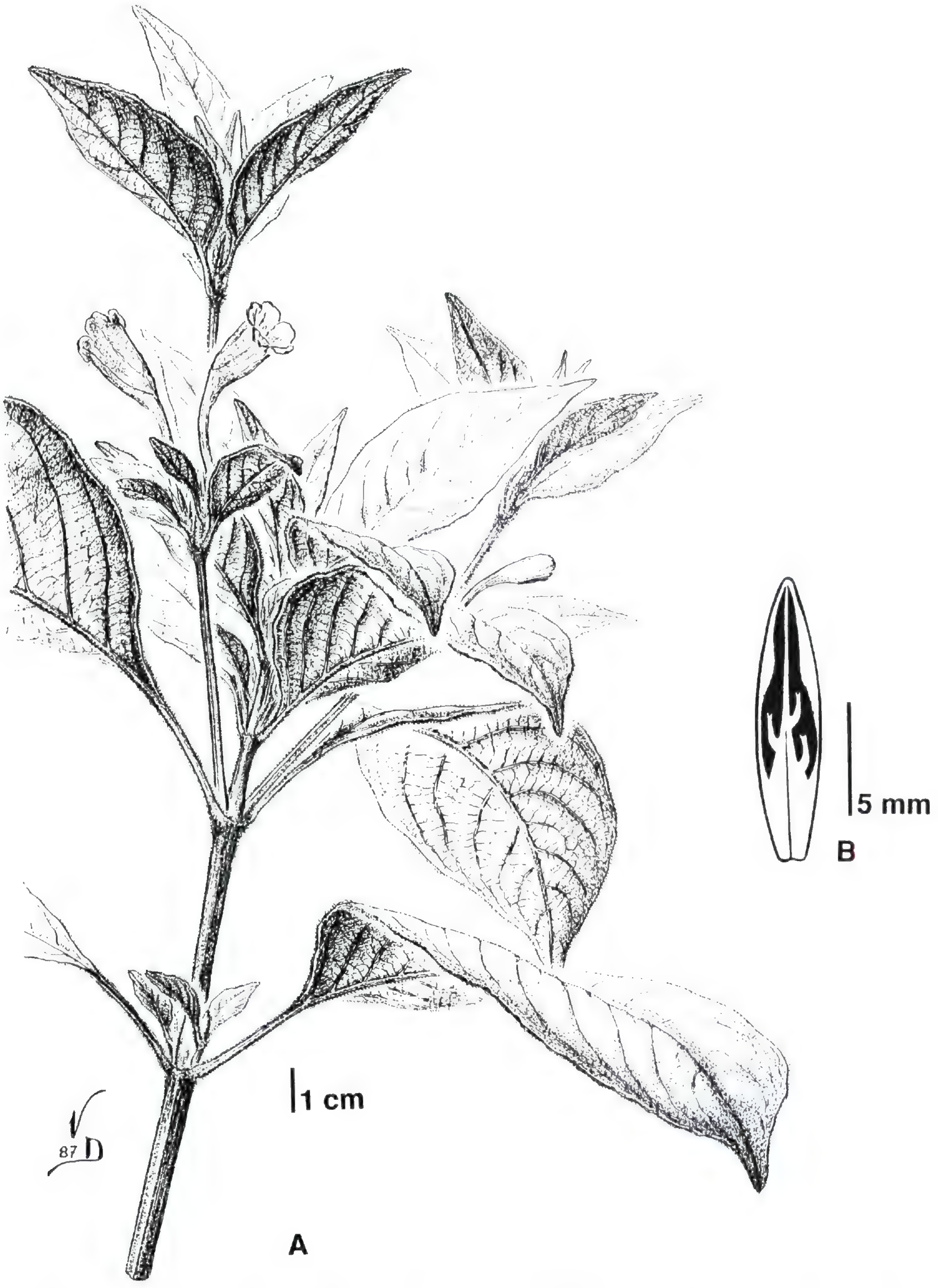


FIGURE 10. *Ruellia sanguinea* Griseb.—A. Flowering branch.—B. Open capsule without seeds, schematic. (A, *Fabris 4491*; B, *Iudica & Ramadori 355*.)

*Distribution.* Southern Bolivia and northern Argentina, in the north of Salta and east of Jujuy. It is found growing in the shade of mountain forests of the Yungas phytogeographical province, between 600 and 2,000 m altitude. It flowers in spring and autumn, especially in October and May.

*Representative specimens.* ARGENTINA. **Jujuy:** Serranía de Calilegua, *Fabris 4478, 4491* (LP); Río de Las Piedras, *Iudica & Ramadori 355* (SI). **Salta:** Depto. Orán, Río Santa María, las Juntas, *Castellanos 29* (BA, LIL); Parque Nacional Baritú, Arroyo Sidras, *Brown 2003* (SI); 8 km antes de Porongal, *Cuezzo 9213* (LIL).

*Ruellia sanguinea* is characterized by the small red corollas with a long basal tube. Though the semi-erect, small lobes and red color of the flowers suggest hummingbird pollination, the narrow, long, basal tube of the corollas and the morphology of the inflorescence separate this taxon from the other red-flowered species in the area. In these characters and in leaf morphology it is quite similar to the white-flowered, probably butterfly-pollinated, *Ruellia puri* Nees, widely distributed throughout central Brazil and western Bolivia. This suggests that the different pollination syndromes in *Ruellia* probably arose many times as parallelisms in the evolution of different lineages.

This species was originally described from northern Argentina (Salta), its name referring to the blood-colored flowers it produces. This name was erroneously used later by most modern authors for *Ruellia angustiflora*, a different red-flowered species, frequent in eastern Paraguay, northeastern Argentina, southern Brazil, and northern Uruguay (Ezcurra, 1989).

## II. Group **Ruellia**

*Ruellia* L. sect. *Euruellia* Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 311. 1895. TYPE: *R. tuberosa* L.

*Cryphiacanthus* Nees, Index Sem. Hort. Vratisl. 1841; Linnaea 16: 298. 1842. TYPE: *C. badensis* Nees, nom. illeg. (= *R. tuberosa* L.).

Flowers pedicellate, borne in dichasial cymes subtended by the upper leaves, rarely reduced to solitary flowers, always pedicellate and bibracteolate. Capsules terete or narrowly elliptic in contour, hollow nearly to the base. Seeds 14–28.

Group *Ruellia* is important in the New World and consists of several weedy, erect or rosettiform herbs that are common in open, low, disturbed, subtropical and tropical areas. In southern South America they are principally found in floristic provinces of the Chaco region or dominion (see Cabrera & Willink, 1980). Many South American species of this group are very similar to species in Central and North America, and could be closely related. The mucilaginous viscid pubescence of the seeds when wetted allows them to be easily carried by migrating birds. This could explain the long-distance disjunctions of "vicariant" species between the Northern and Southern hemispheres.

**7. Ruellia ciliatiflora** Hook., Bot. Mag. 66: tab. 3718. 1840. *Arrhostoxylum ciliatiflorum* (Hook.) Nees, DC. Prodr. 11: 216. 1847. TYPE: Fig. in tab. 3718 of Bot. Mag. 66. 1840. Figure 11.

*Ruellia lorentziana* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 259. 1879. SYNTYPES: Argentina. Tucumán: Tucumán, 22 Dec. 1872 *Lorentz & Hieronymus 176* (GOET not seen, photo SI); Tucumán, *Lorentz & Hieronymus*, 6–22 Dec. 1872 (GOET not seen, photo SI).

Perennial herb 30–80(–100) cm tall, sparsely branched from a subligneous base, with clustered, tough, fibrous roots. Stems erect, obtusely quadrangular, with short glandulous pubescence intermingled with longer simple hairs, glabrescent at maturity. Leaves on pilose petioles 0.5–2.5 cm long, the blade widely ovate, 4–13 cm long and 2–8 cm wide, obtuse and mucronate, widely cuneate to truncate on the base and somewhat decurrent on the petiole, markedly pubescent on the nerves, the surface ± pilose and sometimes glutinose, the margin irregularly and shallowly crenate. Flowers pedicellate, borne in dichasial cymes in the axils of small bracts or reduced apical leaves, aggregated in an ample, terminal pyramidal thyrse, sometimes enriched by lateral thyrses originating on the axils of the upper leaves, the whole appearing paniculate. Bracts foliaceous; bractlets lanceolate, small, and pubescent. Calyx ca. 10 mm long, the segments linear, to 8 mm long, glandulous-pubescent. Chasmogamous flowers tilted, blue, 3.5–4.5 cm long, the basal tube angled on top, 1–2 cm long, the throat 1.5–2 cm long and 1 cm diam., the lobes spreading, obovate, ca. 1 cm long and 1 cm wide, the margin undulate and sometimes ciliate, the anterior lobes with dark palate markings toward the orifice. Stamens included, long filaments ca. 6 mm long, short 4 mm long, the anthers 2 mm long. Ovary and style puberulous. Cleistogamous flowers frequent, reduced, tubular, and closed. Capsule elliptic, 2–3 cm long and 3–5 mm thick, hollow nearly to the base, the surface puberulous. Retinacula 2 mm long; seeds 16–24, pale-colored, 2 mm diam., appressed puberulous when dry and with mucilaginous extended hairs when wet.

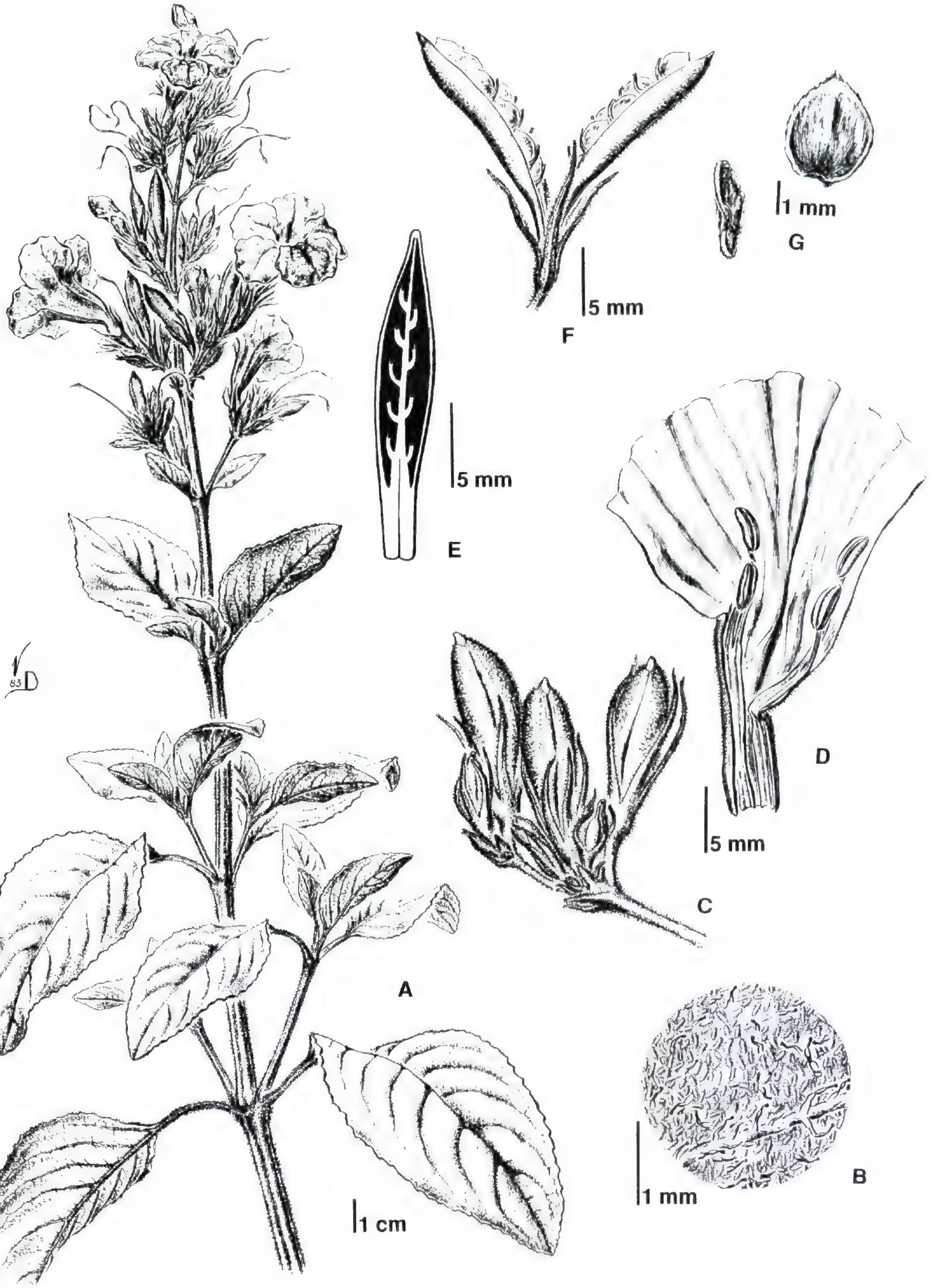


FIGURE 11. *Ruellia ciliatiflora* Hook.—A. Flowering branch.—B. Leaf abaxial surface, showing glandular and eglandular hairs and cystoliths. C. Portion of inflorescence, in fruit.—D. Corolla dorsally open, showing stamens.—E. Open capsule without seeds, schematic.—F. Dehiscent capsule, with seed. G. Seed. (A–D, F, G, *Cabrera 30998*; E, *Kiesling 5566*.)

*Distribution.* Colombia to Bolivia, Paraguay, southwestern Brazil, and northern Argentina, especially in Chaco regions. *Ruellia ciliatiflora* is commonly found growing as a weed in moist, open, disturbed places, such as roadbanks, cultivated or abandoned fields, borders of water courses, dry river beds, clearings of forests, and waste places. It is sometimes cultivated as an ornamental, and prefers sunny locations and sandy soil. It flowers in spring and summer, from October to April, and frequently presents cleistogamous flowers.

*Representative specimens.* ARGENTINA. **Catamarca:** Depto. La Paz, Olta, *Brizuela 700* (US); Depto. Ancasti, Río Chico, *Brizuela 777* (LIL); Depto. Sta. Rosa, Alijilan, *Pierotti 11561* (LIL); Depto. Valle Viejo, San Isidro, *Rojas Paz 37* (LIL). **Chaco:** Presidente Roque Saenz Peña, *Buratovich 469* (LIL, US); Nueva Pompeya, *Flosdorff*, 1 Nov. 1906 (BAB); Taco Pozo, *Meyer 2045* (LIL); Colonia Benítez, *Schulz 2502* (CTES), *9783* (CTES, US); Las Breñas, *Schulz 10812* (CTES); Vilelas, camino al Paranacito, *Schulz 16431* (CTES); Resistencia, *de la Sota 904* (LIL). **Corrientes:** Capital, *Augusto 1* (CTES), *Burkart 68896* (SI), *Maruñak 147* (LP, SPF), *Meyer 6604* (LIL). **Formosa:** Ing. Juárez, orilla S del pueblo, *Arenas 2317* (CTES, SI, US); El Porteño, *Guaglianone 538* (SI); Ruta 90 al S de Pirané, *Guaglianone 662* (SI); Laishi, *Jorgensen 2845* (BA, LIL, SI, US); Depto. Patiño, a orillas del Río Pilcomayo, *Krapovickas 1219* (LIL, LP, SI); Pirané, *Morel 129* (LIL); 3 km al SE de Espinillo, *Morel 7224, 7291* (LIL, US); 36 km W de Palo Santo, *Petetín 1650* (BAB); Herradura, costa del Río Paraguay, *Piccinini 3401* (BAB, SI); Comandante Fontana, *Schulz 17023* (CTES); Nuevo Porteño, *Schulz 17979* (CTES). **Jujuy:** Estación Margarita Verón, *Araque & Barkley 1999Ar489* (LIL); La Mendieta, *Cabrera 16396, 21166* (LP); Puente del Río San Francisco, *Cabrera 20348* (LP); Entre Punta del Agua y Palma Sola, *Cabrera 30998* (SI); Palmar de San Francisco, *Fabris 3070* (LP); Pampa Blanca, *Fabris 3162* (LP); Dique La Ciénaga, *Fabris 3662* (LP); Palma Sola, *Fabris 5281* (LP); Sierra de Zapla, *Fabris 8275* (LP); Entre Fraile Pintado y Ledesma, *Legname & Cuezzo 5982* (LIL, LP); De El Fuerte a Palma Sola, *Kiesling 5566* (SI); Cerros de San Lucas, *Kiesling 5679* (SI); Laguna San Miguel, *Zuloaga 2825* (SI). **La Rioja:** La Rioja, *Esteban 22* (BAB). **Salta:** Caraparí, *Abiatti & Claps 337* (LP); Coronel Cornejo, *Abiatti & Claps 991* (LP); Coronel Moldes, *Bartlett 19643* (SI); Río Piedras, *Birabén 1409* (LP); Saucelito, sobre Ruta 34, *Cuezzo & Vervoorst 7641* (LIL); Salta Ciudad, *Jorgensen 299* (SI); Río Candelaria, *Legname & Cuezzo 3442* (LIL); General Ballivián, *Maldonado 762* (LP); Padre Lozano, *Malvárez 435* (LIL); Cerrillos, *Meyer 3799* (LIL); Estancia San Jorge, *Pedersen 10820* (CTES); Tobantirenda, *Pierotti 7355* (LIL, US); J. V. González, Finca San Javier, *Saravia Toledo 119* (LIL); Quebradas del Rio Toro y el Río Blanco, *Vattuone 145* (SI); Candelaria, Estación Ruiz de los Llanos, *Schreiter 5796* (LIL); Ruta 34, 10 km de Campichuelo hacia Embarcación, *Zuloaga 2649* (SI, US). **Santiago del Estero:** Yutuyacu, *Legname 77* (LIL); Depto. Ojo de Agua, Pozo Cavado, *Maldonado 933* (LP); Capital, Vuelta de la Barranca, *Meyer 14074* (LIL); Entre el Mojón y Cerro del Remate, *Molina 1800* (BAB); La Banda, *O'Donnell 4259* (LIL, US); Taco Pozo, *Peirano 8998* (LIL); Entre Choya y Estación La Punta, *Piccinini & Petetín 3375* (BAB); Depto. Copo, Los Tigres, *Roic 564* (BAB); Ciudad, *Ulibarri 998* (SI); Depto. Quebrachos, Para Yacu, *Ulibarri 1393* (SI); Depto. Pellegrini, bañados del Río Urueña, *Venturi 5676* (MO, US). **Tucumán:** Depto. Leales, Ruta 9, La Florida, *Krapovickas 17353* (CTES); Capital, Villa Luján, *Venturi 38* (SI, US); Tapia, *Venturi 2402* (BAB, US); Muñecas, *Schreiter 1427* (LIL, US); Depto. Graneros, El Zapallar, *Sotelo 163* (LIL, US), *204* (LIL). PARAGUAY. **Amambay:** zwischen Río Apa und Río Aquidàbán, Estrella, *Fiebrig 4337* (G); in regione cursus superioris fluminis Apa, *Hassler 7944* (BM, G, GH, LIL, MO, NY, P, RB). **Boguerón:** 59 km S del desvío a Loma Plata por ruta Trans-Chaco, *Mereles 3575* (CTES). **Chaco:** Entre Teniente Martínez y Madrejón, ca. Madrejoncito, *Fernández Casas 4313* (G, MO, NY); Mayor Pedro Lagerenza, *Schinini & Bordas 15201* (CTES, G, US). **Presidente Hayes:** in regione cursus inferioribus fluminis Pilcomayo, *Rojas 65* (G); Puerto "Zapatero-Cué," barranca Río Paraguay, *Rojas 2194* (SI); Gran Chaco, ripam occidentalem flum. Paraguay, 23°20′S–23°30′S, *Rojas 2427* (G, GH, MO, NY, P), *7427* (GM, G, P).

*Ruellia ciliatiflora* is a common weed in disturbed places of subtropical South America, especially in western Chaco areas and adjacent regions. This species has generally been known as *Ruellia lorentziana* in Argentina, where it ranges from Jujuy to Santiago del Estero. The name *Ruellia ciliatiflora* precedes *R. lorentziana* and was used to describe plants grown in England from seeds sent by Tweedie from Buenos Aires, Argentina. Although this species does not grow in Buenos Aires, Tweedie probably collected it during his trips to northern Argentina. The beautiful illustration and description in *Botanical Magazine* show clearly that it is the same species. It is closely related to species of the *Ruellia nudiflora* complex from North America.

**8. Ruellia coerulea** Morong in Morong & Britton, Ann. New York Acad. Sci. 7: 193. 1893. TYPE: Paraguay. Pilcomayo River, 1888–1890, *Morong 1013* (holotype, NY; isotypes, MO, US). Figure 12.

*Arrhostoxylon microphyllum* Nees in C. Martius, Fl. Bras. 9: 22. 1847. *Ruellia microphylla* (Nees) Lindau, Engl. Bot. Jahrb. 19 Beibl. 48: 16. 1894, not Cavanilles, 1801. TYPE: Uruguay. Montevideo: ad S. Luciam sub fruticibus ripas fluviorum obumbrantibus, *Sellow s.n.* (holotype, B destroyed; isotypes not found). Syn. nov.

*Cryphiacanthus angustifolius* Nees in DC., Prodr. 11: 199. 1847, not *Ruellia angustifolia* Swartz, 1788. *Ruellia spectabilis* Britton, Ann. New York Acad. Sci. 7: 192. 1893, not Nicholson, 1886. *Ruellia ignorantiae* Herter, Rev. Sudamer. Bot. 4: 193. 1937. *Ruellia tweediana* Griseb. ex Fernald, Rhodora 47: 13, pl. 840. 1945. TYPE: Argentina. Entre Ríos: without locality, *Tweedie s.n.* (lectotype, K). Syn. nov.

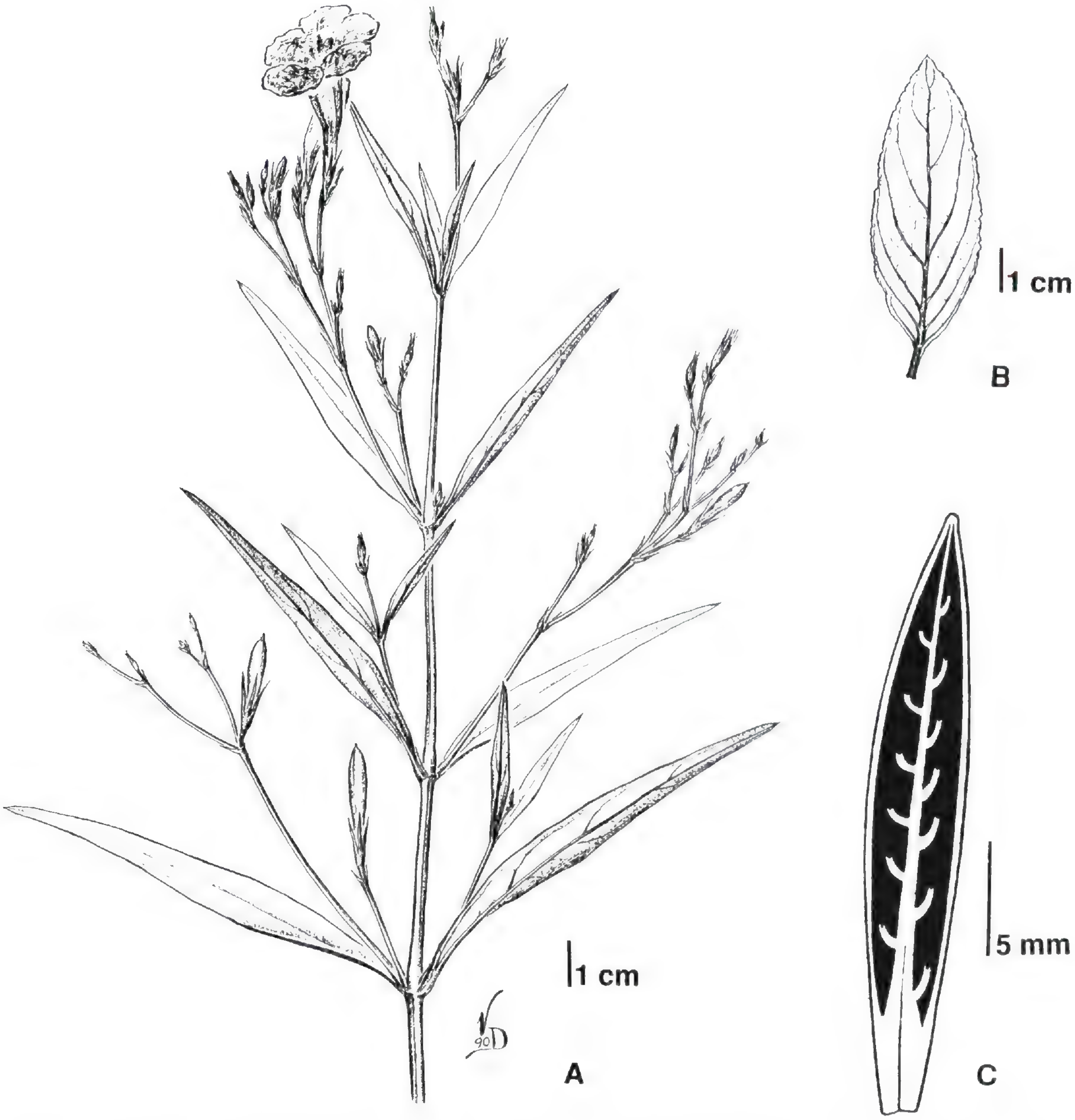


FIGURE 12. *Ruellia coerulea* Morong.—A. Flowering branch.—B. Leaf shape of a plant of another population, to show variation in this character.—C. Open capsule without seeds, schematic. (A, *Hassler 1661*; B, *Venturi 632*; C, *Krapovickas 11804*.)

Sparsely branched erect herb 30–120 cm tall, with fibrous roots from a basal rhizome; stems ascending, subtetragonous, glabrous, sometimes ciliate at the nodes. Leaves on short, ciliate petioles, the blades ovate or elliptic to narrowly oblong or lanceolate, 5–12 cm long, 0.3–1.5 cm wide, the lower ones generally shorter and wider than the upper, all obtuse at the apex, cuneate at the base, the margins entire, completely glabrous, with numerous sessile glands on the lower surface. Flowers on glabrous pedicels, borne in pedunculate, few-flowered, dichotomous cymes, in the axils of alternately one of each pair of the uppermost leaves, rarely on both; bracteoles glabrous, linear, and small. Calyx of chasmogamous flowers 0.7–1.5 cm long, the segments linear-lanceolate, acute, glandulose-puberulous. Chasmogamous corollas tilted, blue or whitish, 3–4 cm long, the basal tube 0.5–1 cm long, the throat obconic, 1.5–2 cm long and ca. 8 mm wide in the orifice, with palate markings in the lower side, the lobes suborbicular, ca. 1 cm diam. Cleistogamous corollas reduced and closed. Stamens included. Ovary and style glabrous. Capsule narrowly elliptic or oblong, 2–2.5 cm long and 4 mm thick, hollow nearly to the base, glabrous; retinacula acute. Seeds 16–24, 2–3 mm

wide, appressed pilose when dry and viscid when wet.

*Distribution.* Western Bolivia, Paraguay, Uruguay, and northeastern Argentina, and limiting areas of southern Brazil, in open areas of eastern Chaco and adjacent phytogeographical regions. It is found in wet or periodically flooded, sunny places, such as ditches, streams, riverside lawns, or temporarily inundated areas. It flowers in spring and summer, from September to February.

*Representative specimens.* ARGENTINA. **Chaco:** Napalpí-Machagai, *Malvárez 839* (LIL), Las Breñas, *Malvárez 942* (LIL); Fontana, *Meyer 542* (LIL); Barranqueras, *Birabén 78* (LP); *Meyer 16243* (LIL); Depto. Güemes, 10 km S de Misión Nueva Pompeya, *Molina & Sánchez 2108* (BAB); Est. Experimental INTA Roque Saenz Peña, *Molina & Sánchez 2394* (BAB); Fuerte Esperanza, *Piccinini & Hilfer 4158* (BAB); Entre Saenz Peña y Tres Isletas, *Ragonese y Castiglione 6930* (LP); Colonia Benítez, *Schulz 140* (SI), *14147* (BAB); Depto. San Martín, de Laguna Limpia a Presidente Roca, *Schulz 2530* (BAB, US); Depto. Mayor Fontana, Enrique Urien, *Schulz 17774* (BAB, US). **Córdoba:** Río I, Obispo Trejo, *Balegno 1085* (LIL); Orillas Mar Chiquita, *Stuckert 23141* (LIL). **Corrientes:** Goya, *Boelcke 1530* (SI); Curuzú Cuatiá, *Birabén 5170* (LP); Río Guayquiraró, 18 km al S de Sauce, *Cristóbal 1562* (CTES); Depto. Monte Caseros, Juan Pujol, *Ibarrola 2343* (LIL); 25 km E de San Luis del Palmar, *Krapovickas & Cristóbal 11804* (SI, US); 4 km E de Paso de La Patria, *Krapovickas & Cristóbal 14931* (CTES, SI); Las Marías, 7 km al S de Gobernador Virasoro, *Krapovickas 16790* (CTES); 8 km al N de Carlos Pellegrini, *Krapovickas 20080* (CTES); Río Santa Lucía, Paso Naranjito, *Krapovickas 24562* (CTES); Depto. Empedrado, Estancia La Yela, *Pedersen 10833* (CTES, NY); Puente sobre el Río Miriñay, sobre Ruta 123, *Schulz 18641* (CTES); 40 km N de Curuzú Cuatiá hacia Mercedes, *Zuloaga 3355* (SI). **Entre Ríos:** Concepción del Uruguay, *Baez 61* (LP); Gualeguaychú, *Burkart 4270* (SI); La Paz, *Burkart 21418* (SI); Concordia, Parque Rivadavia, *Burkart 21926* (SI); Colón, Arroyo del Medio, *Meyer 10564* (LIL); Salto Grande, *Troncoso 1292* (SI); Federación, Chaviyú, *Troncoso 1575* (SI). **Formosa:** Ingeniero Juárez, toldería Toba 1 km N del pueblo, *Arenas 2274* (SI, US), Estanislao del Campo, *Cabral 603* (BAB); Parque Nac. Pilcomayo, alrededores casa guardaparque, *Cusato 736* (BAB); Entre Bartolomé de Las Casas y Los Matacos, *Eliseten-Cano 174* (BAB); Ruta 81, alrededores de Bosch, *Fortunato 412* (BAB); alrededores de Palo Santo, *Petetín 1594* (BAB); Depto. Pilcomayo, Laguna Blanca, *Piccinini & Leguizamón 2510* (BAB); Herradura, costa del Río Paraguay, *Piccinini & Petetín 3439* (BAB); Las Lomitas, *Krapovickas 1310* (SI); Depto. Pilagá, 3 km W de Espinillo, *Morel 9269* (LIL); El Colorado, Estación INTA, barranca alta del Río Bermejo, *Schulz 17546* (CTES); Nuevo Porteño, *Schulz 17973* (CTES); Estación Palo Santo, 139 km NW de Formosa, *West 8472* (SI). **Jujuy:** Ruta 1 de Aguas Calientes a El Piquete, Laguna San Miguel, *Cabrera 21671* (LP, SI), *Zuloaga 2826* (SI). **Misiones:** San Ignacio, Tabetuy, *Bertoni 52* (LIL); Candelaria, *Descole 3257* (LIL); Santa Ana, Balneario Municipal, *Zuloaga 3179* (SI). **Salta:** Nuestra Señora de Talavera, *Cuezzo & Morello 257* (LIL); Embarcación, Palmar de Laguna San José, *Hueck 81* (LIL); El Quebrachal, *Luna 705* (LIL); Joaquín V. González, *Saravia-Toledo 139* (LIL); Capital, Cerro San Bernardo, *Sotelo 837* (LIL); 10 km de Campichuelo hacia Embarcación, *Zuloaga 2650, 2651* (SI). **Santiago del Estero:** Silipica, frente a La Porteña, *Argañaraz 297* (BA); Entre Añatuya y Colonia Dora, *Castiglione & Ragonese 7788* (LP); Depto. Pellegrini, Algarrobal Viejo, *Luna 371* (LIL); Totora Pampa, camino a Atamisqui, entre Ruta 9 antigua y Arroyo Sunchal, *Piccinini & Petetín 3195* (BAB); Depto. Copo, Los Tigres, *Roic 424* (LIL), *604* (BAB, LIL); Depto. Pellegrini, Bañado del Río Urueña, *Venturi 5675* (LIL, SI, US). **Santa Fé:** Tostado, Río Salado, *Job 1137* (LP), *Schulz 1262* (LIL); Villa Guillermina, *Meyer 2841* (LIL); Lanteri, Arroyo El Rey, *Núñez & Rivas 93* (LP); Villa Ana, Estero La Julia, *Quarín 757* (CTES); Depto. Garay, Col. Mascías, *Spegazzini 154* (BAB); Mocoví, Amores, *Venturi ss158* (BA, SI, US). **Tucumán:** Depto. Leales, Chañar Pozo, *Venturi 632* (BA, BAB, LIL, SI, US), *685* (BA, LIL, SI). BRAZIL. **Rio Grande do Sul:** Porto Alegre a Canoas, *Augusto 18894* (ICN); São Gabriel, Rio Vacacaé, *Palacios & Cuezzo 1572* (LIL). PARAGUAY. **Amambay:** zwischen Río Apa und Río Aquidabán, *Fiebrig 4338* (G), *4893* (BM, G, K); in cursus superioris fluminis Apa, *Hassler 8031* (BM, G, NY). **Boguerón:** Paratodo, *Arenas 471* (CTES), *1265* (SI, US); Filadelfia, *Hahn 786, 1859* (G, MO, US); Pozo Arias, *Mereles 495* (CTES, G); Presidente Ochoa, *Mereles 2264* (G); Ruta Transchaco, 22°35′S, 59°50′W, *Schinini & Palacios 25802* (G); Mariscal Estigarribia, Ocho Cué, *Schmeda 163* (G). **Central:** Base du Cerro Lambaré, *Balansa 2452a* (P), Plaine d'Aregua, *Balansa 2452b* (P); ad ripam rivi Juqueri, *Hassler 1533* (G); Orillas Río Salado, *Rojas 1661* (LIL, SI); Tacuaral, *Hassler 3820* (G); Trinidad-Asunción, *Schinini 3524* (CTES). **Chaco:** Entre Teniente Martínez y Madrejón, *Fernández Casas 4318* (G, NY); Cerca de Pozo Colorado, *Fernández Casas 4492* (NY); Mayor Pedro Lagerenza, Río Timane, *Schinini & Bordas 14865* (CTES), *15200* (CTES, US), *15211* (CTES); Cerro León, *Schinini & Bordas 18002* (CTES, G, US). **Concepción:** Concepción, *Hassler 7416* (G, GH, K, P). **Cordillera:** 2 km NE de Río Salado, de Limpio a Emboscada, *Arbo 1640* (CTES, G). **Guairá:** Plaine de Doña Juana, *Balansa 2452* (G, P); Tebicuary, *Mereles 2307* (G). **Neembucú:** Pilar, *Meyer 16100* (LIL). **Nueva Asunción:** Ruta Trans-Chaco, 21°30′S, 61°15′W, *Schinini & Bordas 16511* (CTES). **Paraguarí:** Paraguarí, *Fiebrig 890* (B, G, GH); *Sparre & Vervoorst 600* (LIL). **Presidente Hayes:** Estancia Loma Pyta, *Arenas 670* (NY); Estación Experimental MAG, *Bernardi 20103* (MO, G); Ruta Transchaco, pk 189, *Billiet & Jadin 3035* (BM, MO, NY); 30 km NW de Pozo Colorado, *Fernández Casas 4464* (G, NY); Río Verde, cerca de Pozo Colorado, *Fernández Casas 4492* (MO); Ruta Transchaco, km 50, *Mereles 757* (CTES, G); Estancia La Perla, *Pedersen 14620* (G); in regione cursus inferioris fl. Pilcomayo, *Rojas 64* (BM, G), *314, 314a* (G); Ripam occidentalem fl. Paraguay, *Rojas 2872* (BM, G). **San Pedro:** Colonia Primavera, *Woolston 800* (K, LIL, NY, SI), *927* (NY, US). **Without locality:** *Hassler 8031* (BM, MO). URUGUAY. **Artigas:** Río Uruguay y Arroyo Itacumbú, *Rosengurtt 10459* (MVFA). **Canelones:** Santa Lucía, *Gallinal B 186* (US), *Marchesi 1307* (MVFA). **Florida:** Santa Lucía Chico, *Berro 1732* (MVFA, US). **Montevideo:** Santa Lucía, *Arechavaleta 3108/4788* (SI). **Rivera:** Cuñapiru, *Wright 1928* (BM). **Tacuarembó:**

Tacuarembó, *Berro 4824* (MVFA). **Treinta y Tres:** Ciudad Treinta y Tres, *Rosengurtt 10662* (MVFA). **Without department:** Bois de Sainte Lucie, *Fruchard s.n.* (P).

*Ruellia coerulea* is characterized by the blue-flowered axillary cymes and glabrous habit, and is common in seasonally inundated areas of subtropical South America. It appears clearly related to *Ruellia brittoniana* and *Ruellia malacosperma* of southern North America. Like many semiaquatic plants, it shows much variation in leaf shape and leaf area, probably subject to environmental influence. This variation may also be the result of introgression with the common *Ruellia ciliatiflora* in areas where they grow sympatrically.

*Ruellia coerulea* shows an extended range in subtropical South America and also varies in habit. The plants from the northern portions of its range (eastern Bolivia, northwestern Paraguay, and western Brazil) generally have larger and more woody stems, and present a more fruticose habit. The plants from the southernmost portion of its range (Uruguay) are frequently small, delicate herbs. This may be related to climatic variations associated with latitude and seasonality, especially temperature and photoperiod.

Fernald discussed part of the nomenclatural problems of this species when he validated the name *Ruellia tweediana*. This name has been the one most used for this species (e.g., Dawson, 1979; Piovano & Bernardello, 1991), but the epithet *coerulea* precedes it. *Ruellia microphylla* has also been used for the identification of material from Paraguay. Although the type of *Arrhostoxylon microphyllum*, its basionym, was destroyed at Berlin and no isotypes have been found, the original description by Nees of the material from Montevideo, Uruguay, clearly depicts a plant of the weaker, southernmost form of *Ruellia coerulea*.

A few specimens collected in Paraguay show morphological intermediacy with *Ruellia brevicaulis*, suggesting hybridization.

**8a. Ruellia coerulea** Morong × **Ruellia brevicaulis** (Nees) Lindau.

Plants resembling *Ruellia coerulea*, with pedunculate axillary inflorescences, the flowers pedicellate and bibracteolate, but with shorter stems and wider, ovate, somewhat serrulate, pilose leaves, the trichomes shiny and extended as in *Ruellia brevicaulis*.

*Representative specimens.* PARAGUAY. **San Pedro:** Alto Paraguay, *Woolston 118* (SI); Primavera, *Woolston 989, 1252* (US). **Canendiyú:** iter ad Yerbales Sierra de Maracayú, in regione vicine San Estanislao, *Hassler 4281* (G, P, NY); Sierra de Maracayú, *Hassler 5092* pro parte (BM, NY).

These specimens are morphologically intermediate between *Ruellia coerulea* and *R. brevicaulis*, of group *Dipteracanthus*. They all have been collected in eastern Paraguay, where the areas of these species are sympatric, and appear to be the product of hybridization.

**9. Ruellia macrosolen** Lillo ex Ezcurra, Syst. Bot. 14(3): 297. 1989. TYPE: Argentina. Jujuy: San Pedro de Jujuy, 600 m, 10 Apr. 1926, *Schreiter 5211* (holotype, LIL; isotypes, BA, LP, US). Figure 13.

Low perennial herb 20–40(–60) cm tall, with fibrous, fusiform, tuberous roots; stems ascending, sparsely branched, subtetragonous, pilose and shortly glandulose-pubescent, somewhat glabrescent at maturity, growing from a short horizontal underground rhizome. Leaves on pilose petioles 0.3–2 cm long, the blades thin, ovate or elliptic, mostly 2.5–7 cm long and 1.5–4 cm wide, rounded or obtuse at the apex, cuneate at the base and somewhat decurrent on the petiole, the margins entire or slightly crenate, undulate, the surface pilose on the principal veins. Flowers on glandular pedicels, borne in terminal and axillary, lax, pedunculate, few-flowered dichotomous cymes, aggregated in thyrses and often appearing paniculate; bracts foliaceous, pilose; bracteoles glandular, linear, and small. Calyx 1.5–2 cm long, the segments linear and acute, densely glandular-pubescent. Corollas erect, white, regular, the basal tube 2.5–5 cm long, 2–3 mm diam., the throat 1.5–3 cm long, tinted with grayish mauve at the base, expanding to 1 cm wide at the orifice, the lobes rounded, ca. 1.5 cm long and wide, often emarginate, somewhat undulate in the margins, with faint grayish mauve markings toward the orifice of the throat. Cleistogamous flowers frequent, reduced, tubular, and closed. Stamens 4, included, with filaments ca. 7 mm long and anthers 5 mm long. Style 3–5 cm long, glabrous; ovary pubescent, with a few glandular hairs. Capsules elliptical, 2.5–3.5 cm long and 6–8 mm thick, broadest at or above the middle, hollow nearly to the base, densely and shortly puberulent on the surface; pedicels accrescent at maturity. Retinacula obtuse, 2 mm long. Seeds 12–22, flat, suborbicular, 3 mm long and 2.5 mm wide, appressed-pilose when dry and with hygroscopic-viscid pubescence all over their surface when wet.

*Distribution.* Southeastern Bolivia, western

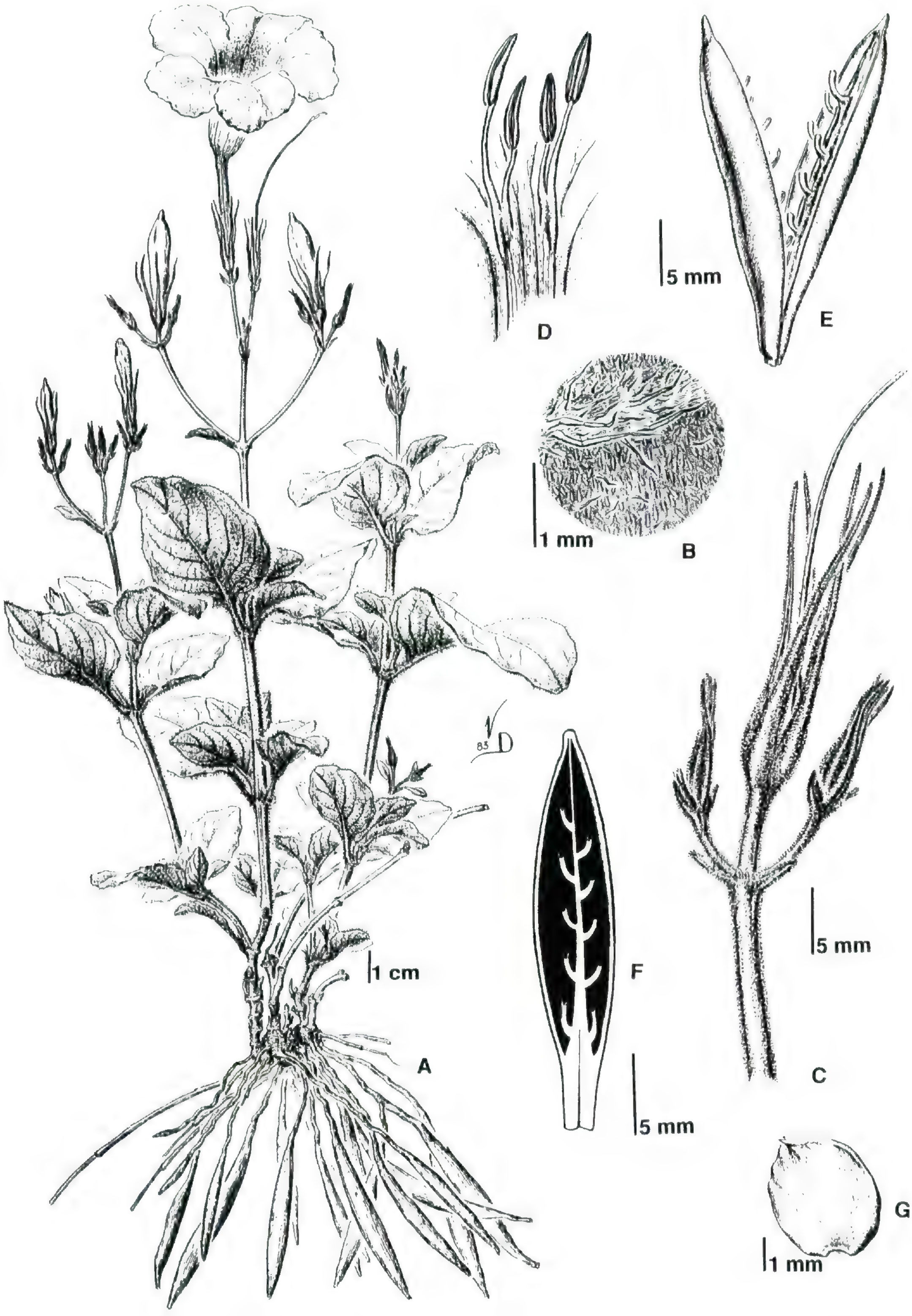


FIGURE 13. *Ruellia macrosolen* Lillo ex Ezcurra.—A. Habit.—B. Abaxial leaf surface, pilose on principal veins.—C. Inflorescence portion with glandular calyces and bracteoles.—D. Stamens.—E. Dehiscent capsule.—F. Open capsule without seeds, schematic.—G. Seed. (A–G, *Pedersen 10818*; F, *Ezcurra & de Azkue 471*.)

Paraguay, and northern Argentina, in regions of western Chaco and adjacent transitional forests. It is found in open and often disturbed places such as sandy roadbanks, abandoned fields, borders or clearings in forests, and margins of streams, from 300 to 900 m elevation. It flowers in spring and summer, from December to February.

*Representative specimens.* ARGENTINA. **Chaco:** Napalpí, en orillas camino a Choritotipo, *Donat 48* (LP); 43 km de Fuerte Esperanza hacia Castelli, *Molina & Sánchez 2156* (BAB); Taco Pozo, *Peirano 8997* (LIL); Fte. Esperanza, *Piccinini & Hilfer 4149* (BAB); Las Breñas, *Schulz 780* (CTES); Gancedo, *Schulz 996* (LIL); Villa Angela, *Schulz 2542* (CTES). **Formosa:** Patiño, 17 km al N de Estanislao del Campo por Ruta 81, *Molina 1223* (BAB); Matacos, Ingeniero Juárez, *Schulz 9713* (CTES). **Jujuy:** Huaico Hondo, *Ahumada 4535* (CTES, SI); Pampa Blanca, *Birabén 1471* (LP), *Cabrera 15556* (LP); camino a El Cadillal, *Cabrera 29947* (SI); alrededores Aeropuerto, al SE de Perico, *Ezcurra & de Azkue 471* (SI); Ledesma *Fabris & Zuloaga 7683* (LP); Cerca de Fraile Pintado, *Legname & Cuezzo 5947* (LIL, LP); Cerro de San Pedro, *Venturi 5174* (SI, US); Sierra de Calilegua, *Venturi 10773* (SI); de Aeropuerto El Cadillal a empalme con ruta 34, *Zuloaga 2993* (SI). **Salta:** Entre Gaona y El Quebrachal, *Castiglione & Ragonese 6710* (BAB, LP); Campo Santo, Yaquiasmé, *Cuezzo 4969* (LIL); Joaquín V. González, *Krapovickas 1717* (LIL); Güemes, arroyo Saladillo, *Krapovickas & Cristóbal 17416* (CTES); Anta, El Quebrachal, *Malvárez 620* (LIL, US); Entre Rosario de la Frontera y Metán, *Meyer 22698* (LIL); Almirante Brown, *O'Donell 5394* (LIL, US); Anta, Estancia San Jorge, *Pedersen 10818* (CTES, LP); La Candelaria, *Schreiter 9361* (BA, LIL); Rosario de la Frontera, de Santa Rosa a El Morenillo, *Schreiter 10132* (SI); Entre La Viña y Alemanía, *Schreiter 11516* (LIL); de Las Piedras a Río Juramento por Lumbreras, *Schulz 6574* (CTES, US). **Santiago del Estero:** Cerro del Remate, 550 m, *Venturi 5665* (LIL, US); Depto. Gimenez, El Charco, *Venturi 10200* (MO). **Tucumán:** Vipos, 17 Mar. 1939, *Birabén & Birabén 1536* (LP); Burruyacu, *de la Sota 1384* (LIL), *Venturi 7499* (US); Cerro del Campo, *Venturi 7662* (MO, US); Gobernador Garmendía, *Villa Carenzo 417, 420* (LIL). PARAGUAY. **Amambay:** zwischen Río Apa und Río Aquidaban, *Fiebrig 4512, 4543* (BM, G). **Boquerón:** Estación Experimental Filadelfia, *Vanni 2543* (CTES). **Chaco:** Capitán P. Lagerenza, ca. del puente del Río Timane, *Charpin & Ramella 21577* (G); Parque Nacional Defensores del Chaco, *Duré 441* (CTES); Mayor Pedro Lagerenza, *Schinini & Bordas 15078* (CTES, US); Río Timane, *Schinini & Bordas 15206* (CTES, US); cauce seco del Río Timane, *Spichiger 2787* (US); Agua Dulce, *Shinini & Bordas 18083* (G). **Nueva Asunción:** Ruta Trans Chaco, *Schinini & Bordas 16550* (CTES).

*Ruellia macrosolen* is characterized by the white, nocturnal, sphingophilous flowers with a long basal tube. It seems closely related to the melitophilous, diurnal, blue-flowered *Ruellia ciliatiflora*, and is partially sympatric with it. They are probably genetically isolated through different pollen vectors (Ezcurra, 1989).

**10. Ruellia hygrophila** C. Martius, Flora 24, Beibl. 2(5): 65. 1841. *Lychniothyrsus hygrophilus* (C. Martius) Bremek., Bull. Torrey Bot. Club 75: 669. 1948. TYPE: Brazil. Without locality, 1839, *Martius Herb. Fl. Brasil. 580* (holotype, BR not seen; isotype, NY). Figure 14.

*Cryphiacanthus udus* Nees in C. Martius, Fl. Bras. 9: 49. 1847. TYPE: Brazil. Mato Grosso: prope Cuiabá, *Riedel s.n.* (holotype, LE not seen, photo SI). Syn. nov.

Low perennial, acaulescent herb, with a short basal vertical rhizome, and thick, fibrous roots. Leaves clustered in a rosette, shortly petiolate, obovate, 3–9 cm long and 1–3 cm wide, obtuse and rounded in the apex, the blade decurrent on the petiole; margins entire or somewhat crenate, surface glabrous or slightly hirsute. Flowers borne on lax, multiflowered, anisocaulous, elongate dichasia, appearing somewhat racemiform. Cymes to 15 cm long; peduncles puberulous, to 8 cm long; bracteoles linear and small; pedicels puberulous. Calyx 1–1.5 cm long, the segments linear, acute, 0.8–1.3 cm long, short-pilose, ciliate in the margins. Corolla pale blue, 3–5 cm long, the basal tube 1–1.5 cm long and 2 mm wide, obconic throat 1.2–1.5 cm long and 8 mm diam., the lobes reflexed, suborbicular, 1–1.5 cm diam. Stamens included with anthers ca. 2 mm long. Capsule narrowly elliptic, approximately the same length as the calyx, 1–1.5 cm long and 3 mm diam., hollow nearly to the base. Retinacula less than 2 mm long; seeds 14–16, approximately 2 mm long, adpressed-pilose on the entire surface, the hairs extended and mucous when wet.

*Distribution.* Southeastern Bolivia, southwestern Brazil, Paraguay, northeastern Argentina, and northwestern Uruguay. It is common in borders and clearings of open Chaco xerophilous forests and in palm formations, on hard clay and perodically flooded soil. It flowers in spring and summer, from October to March.

*Representative specimens.* ARGENTINA. **Chaco:** Fontana, *Meyer 2238* (LIL); Colonia Benítez, *Schulz 227* (SI), *779, 2948, 16342, 16352, 16414* (all CTES), *17158* (CTES, US); La Clotilde, al S de Saenz Peña, *Schulz 8164* (CTES, LIL); Las Breñas, *Schulz 10633* (CTES); Depto. 12 de Octubre, General Pinedo, *Schulz 11279* (CTES); Depto. Tapenagá, Cote Lai, *Schulz 14469* (CTES); Depto. Fontana, Enrique Urien, *Schulz 17188* (CTES, US). **Corrientes:** Depto. Capital, Punta Araz, *Arbo & Ferraro* 1530 (CTES, LP); Depto. Capital, arenales del Riachuelo, *Burkart 6843* (SI); Perugorria, *Cabrera 10565* (LP); alrededores de Capital, *Hicken 19932* (SI), *Mar-*

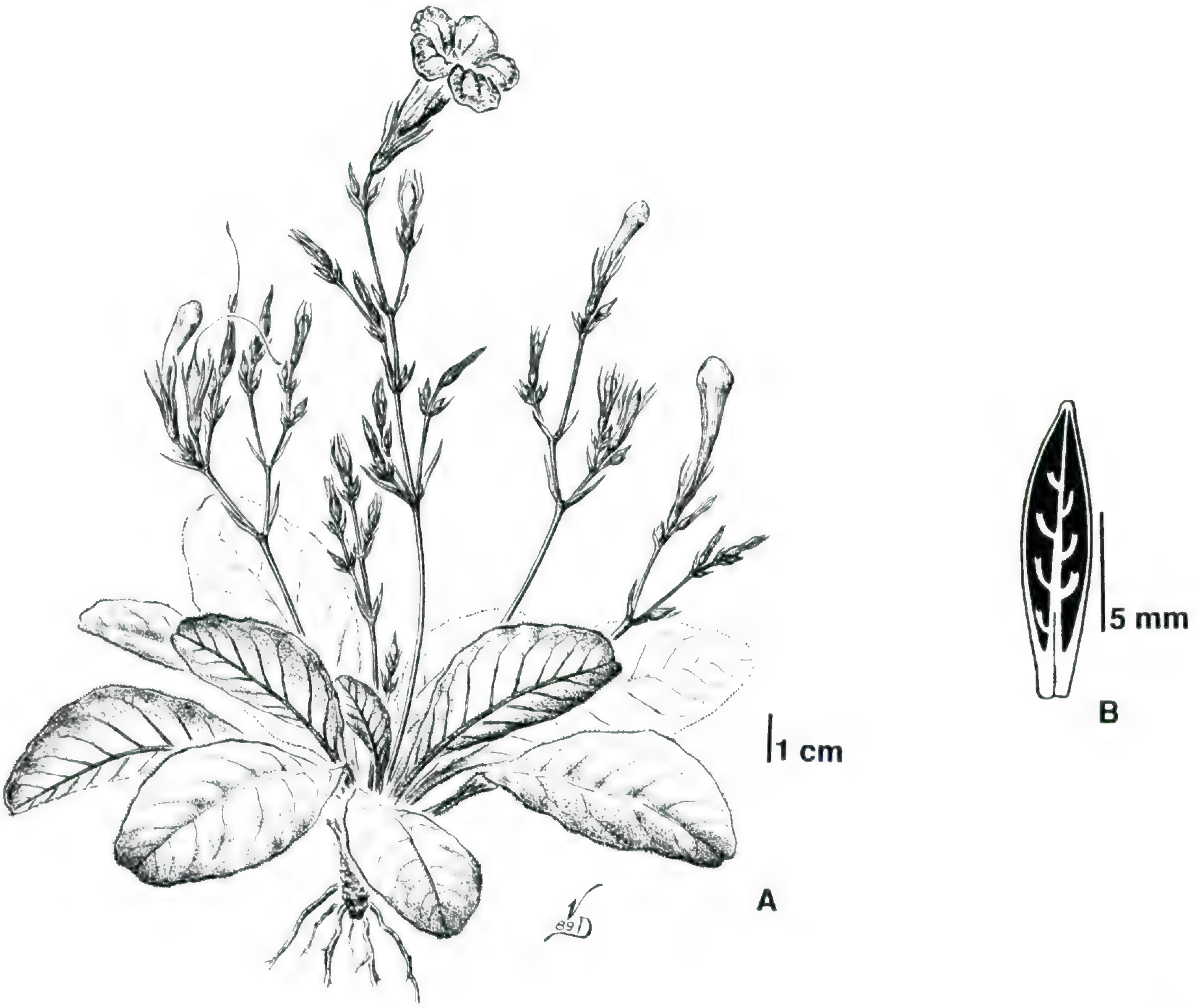


FIGURE 14. *Ruellia hygrophila* C. Martius. — A. Habit. B. Open capsule without seeds, schematic. (A, *Schinini & Bordas 18100*; B, *Arenas 2359*.)

*tínez & Schinini 10392* (CTES), *Meyer 5895* (LIL); Curuzú Cuatiá, *Martínez Crovetto 8419* (BAB), *Spegazzini*, 24 Apr. 1940 (BAB); San Luis del Palmar, *Mroginski 467* (CTES); Depto. Mercedes, 14 km W de Yofre, *Schulz 18506* (CTES). **Formosa:** Matacos, G. N. Juárez, Barrio Obrero, *Arenas 2359* (SI); Bartolomé de las Casas, *Eliseth-Cano 172* (BAB); 4 km S de Ingeniero Juárez, *Fortunato 245, 258* (BAB); 6 km al N de Las Lomitas, *Fortunato 449* (BAB); Formosa, *Jorgensen 2843* (BA, LIL, SI, US); Depto. Pirané, Los Matacos, *Morel 697* (LIL, US); Pozo del Tigre, *Parodi 8500* (LIL); Depto. Pirané, Ruta 81, W de Palo Santo, *Petetin & Molina 1361* (BAB); Depto. Patiño, Ruta 24, a 10 km de Ruta 81, *Petetin 1821* (BAB); Depto. Patiño, Las Lomitas, *Schinini & Pire 24212* (CTES); 15 km W de Las Lomitas, *Schinini 24256* (CTES); Comandante Fontana, *Schulz 17015* (CTES); Bartolomé de Las Casas, *Schulz 17608* (CTES); Nuevo Porteño, *Schulz 17968* (CTES, US). **Misiones:** San Ignacio, Campos, *Alboff*, 22 Nov. 1894 (LP). **Salta:** Depto. Rivadavia, El Tordillo, *Maranta 77* (US). **Santa Fe:** De Reconquista a Nicanor Molina, *Job 884* (LP); Depto. Gral. Obligado, Lanteri, *Maldonado B. 1650* (LP); Villa Guillermina, *Meyer 2840, 3269* (LIL); Depto. Vera, Santa Lucía, *Tecone 4929* (LP). **Santiago del Estero:** Capital, Los Tigres, *Meyer & Vaca 23284* (LIL), *Roic 423* (BAB, LIL). PARAGUAY. **Alto Paraguay:** Puerto Casado, *Rojas 2197* (SI). **Amambay:** zwischen Río Apa und Río Aquidabán, *Fiebrig 4327* (BM, G, GH). **Boquerón:** Mariscal Estigarribia, *Mereles 2245* (G); Alfredo Stroessner, *Spichiger 2072* (US). **Central:** Juqueri, *Hassler 1532* (G); Areguá, ca. Lago Ypacari, *Mereles 1735* (G); Patiño (Nueva Asunción), *Teague 608* (GM). **Concepción:** Prope Concepción, *Hassler 7330* (BM, G, GH, LIL, NY); Puerto Risso, *Meyer 18721* pro parte (LIL); 19 km N de Concepción camino a Loreto, *Vanni 352* (CTES). **Cordillera:** In regine Cordillerae centralis, *Hassler 6507* (BM, G, NY, P). **Chaco:** Parque Nacional Defensores del Chaco, *Duré 426* (CTES); Cerro León, *Schinini & Bordas 17886* (CTES, US); Agua Dulce, *Schinini & Bordas 18100* (CTES, US). **Guairá:** prope Villa Rica, *Balansa 2461* (G, P). **Paraguarí:** Paraguarí, *Balansa 2460* (G, P), *Fiebrig 918* (BM, G, GH); Cerro Hu, *Sparre & Vervoorst 563* (LIL). **Presidente Hayes:** Cursus inferioribus fluminis Pilcomayo, *Rojas 6711* (G); Santa Elisa, *Rojas 2670* (BM, G, GH, LIL, MO, NY, P), *Hassler 7330* (BM, G, LIL, MO, P). **San Pedro:** Distr. Lima, Estancia Carumbé, *Pedersen 9357* (GH, SI); Primavera, *Woolston 775* (LIL, NY, SI, US). URUGUAY. **Artigas:** Ruta 30, Arroyo Catalán, Paso Piaui, *Rosengurtt B7173* (MVFA).

FIGURE 15. *Ruellia morongii* Britton. —A. Habit.—B. Open capsule without seeds, schematic. (A, *Burkart 31102*; B, *Burkart 26385*.)

*Ruellia hygrophila* is characterized by a rosette habit combined with multiflowered long-pedunculate pseudoracemes of blue flowers. It differs from the closely allied short-pedunculate, pale-flowered *Ruellia morongii* also by the nearly glabrous pedicels. It is a common species in all eastern Chaco and surrounding areas, in seasonally flooded and periodically dry soil.

**11. Ruellia morongii** Britton in Morong & Britton, Ann. New York Acad. Sci. 7: 192. 1893. *Cryphiacanthus acaulis* Nees in C. Martius, Fl. Bras. 9: 49. 1847, not *Ruellia acaulis* R. Br. 1810. SYNTYPES: Brazil. River Uruguay, *Baud s.n.* (K); Brazil. Without locality, *Sellow s.n.* (isosyntype, K); Brazil. Rio Grande do Sul: River Jacuhy, 1837, *Tweedie 770* (K). Figure 15.

Low perennial herb, acaulescent, with vertical or oblique rhizome, the thick, fasciculated roots fusiform. Leaves in rosette, ovate, oblong-ovate or obovate, 3–10 cm long and 1–3 cm wide, obtuse and rounded in the apex, the blade decurrent on the petiole, margins entire or somewhat crenate, surface glabrous or slightly hirsute on the principal veins. Flowers shortly pedunculate or borne on subsessile, few-flowered dichasia, frequently reduced to a solitary flower with two bracteoles. Peduncles glabrescent, to 3 cm long; bracteoles linear and small; pedicels hirsute-tomentose under the flowers. Calyx 1.2–2.2 cm long, the segments linear, acute, 1–2 cm long and 1–2 mm wide, densely pilose and ciliate in the margins. Corolla white, sometimes with bluish or yellowish tints, 3–5 cm long, the basal tube 1–1.5 cm long and 2 mm wide, the obconic throat 1.2–1.5 cm long and 8 mm diam., the lobes reflexed, suborbicular, 1–1.5 cm diam. Stamens with anthers ca. 3 mm long. Capsule narrowly elliptic, approximately shorter than the calyx, 1.3–1.8 cm long and 3–4 mm diam., hollow nearly to the base. Retinacula less than 2 mm long; seeds 10–14, approximately 2–3 mm long, adpressed-pilose on the entire surface, the hairs extended and mucous when wet.

*Distribution.* Southern Brazil, eastern Paraguay, northeastern Argentina, and Uruguay. *Ruellia morongii* is found in open and sunny places, on rocky or sandy soil, burnt campos, and grassy savannas. It flowers in spring and summer, from October to March.

*Representative specimens.* ARGENTINA. **Corrientes:** Depto. Esquina, 47 km W de Sauce, Ruta 126, *Ahumada 1444* (CTES); Curuzú Cuatiá, *Birabén 5185* (LP), *Ibarrola 2526* (LIL), *Martínez Crovetto 8429* (BAB); La Cruz, *Burkart 7866* (SI); Depto. Curuzú Cuatiá, cerca de Baibiene, *Castellanos BA34509* (BA, LP); Depto. Santo Tomé, Ruta 14, Las Marias, *Krapovickas 17095* (CTES); Depto. Ituzaingó, 15 km E de Ruta 12 camino a San Carlos, *Krapovickas 18146* (CTES); Estancia El Recreo, 21 km E de Bonpland, *Lourteig 2774* (CTES); Ruta 14, 37 km SW de Pellegrini, *Schinini 7778* (CTES, US); 75 km N de Mercedes, Laguna Trin, *Schinini 11646* (CTES), *11784* (CTES, US); Ruta 40, 14 km de Santo Tomé hacia Garruchos, *Zuloaga 3132* (SI). **Entre Ríos:** Arroyo Robledo a Redomón, *Burkart 26061* (SI); Salto Grande, *Burkart 27197, 31102* (SI), *Cabrera 10571* (LP); La Criolla a Los Charrúas, *Burkart 27571* (SI); Depto. Colón, Palmar Grande, *Burkart 26385, 27376* (SI); Federal, *Burkart 28885* (SI); Colonia Eloisa, barra del Mocoretá, *Burkart 29495* (SI); Nueva Escocia, *Cordini 33* (SI); San José de Feliciano, *Nicora 7719* (SI); Federación, *Martínez Crovetto 4702* (BAB). **Misiones:** Apóstoles, *Cabrera 28479* (SI); Posadas a San José, 5 km pasando Arroyo Pindapoy, *Cuezzo 10832* (LIL); San Javier, *Fabris 7386* (LP); San Ignacio, Pastoreo Chico, *Montes 15557* (LIL); Posadas, *Rodriguez 207* (SI); 4 km SW de Santa Ana, *Schinini 5597* (CTES); De Apóstoles a Concepción de la Sierra, Arroyo Las Tunas, *Zuloaga 3254* (SI). BRAZIL. **Rio Grande do Sul:** Pelotas, Capão de Leão, *Amadeu 70* (ICN); Canoas, Campo de Capão do Corvo, *Augusto 18895* (ICN); São Luis, próximo a Rio Icamaqua, *Fleig 116* (ICN); 17 km W de Rosario, BR 290, *Lindeman 8415* (ICN); Vila Manresa prope Porto Alegre, *Rambo 1* (PACA); Arroio dos Ratos prope São Jerónimo, *Rambo 8466* (PACA); Fazenda do Jarau prope Quaraí, *Rambo 26027* (PACA); Porto Alegre, Morro da Gloria, *Rambo 29403* (LIL); Santo Angelo, *Rambo 52041* (PACA); São Luis Gonzaga, *Sehnem 3624* (SI); Uruguaiana, puente sobre Rio Ibicuí, *Sobral 3252* (ICN, MBM). PARAGUAY. **Paraguarí:** Orilla Río Tebicuary, frente a Florida, *Krapovickas 12387* (CTES, US). **San Pedro:** Prope San Estanislao, *Hassler 5997* (G). **Without locality:** common in saline campos, Itupé, *Jorgensen 4125* (MO, NY, SI, US); central Paraguay, *Morong 223* (US), *323* (GH, US). URUGUAY. **Artigas:** Bella Unión, *Castellanos 18371* (LIL, LP), *Herter 4484* (RB); Puerto Bentiú sobre Rio Cuareim, próximo a Bella Unión, *Del Puerto & Marchesi 11380* (MVFA); Santa Rosa Cuareim, *Herter 985* (LIL, NY, MO). **Paysandú:** Meseta Artigas, *Del Puerto & Marchesi 3488* (MVFA); Rivas, *Herter 82946* (US); Chapicuy, *Rosengurtt B 4181* (US). **Salto:** San Antonio, *Rosengurtt B-927* (US); Río Aguapey, Ruta 3, *Rosengurtt B-6773* (MVFA). **Tacuarembó:** Tacuarembó, *Berro 4914* (US), *4958* (MVFA); Arroyo Laureles, *Lema 6904* (MVFA).

*Ruellia morongii* is characterized by having leaves in a rosette and white subsessile flowers. It seems morphologically related to *Ruellia hygrophila*, but is mostly allopatric with this species and inhabits an area more to the east. It is common in sandy, sunny, open areas and burnt savannas, and seems adapted to periodic fires.

## III. Group **Hygrophiloidei**

*Dipteracanthus* (*Hygrophiloidei*) Nees in C. Martius, Fl. Bras. 9: 43. 1847. TYPE: *Dipteracanthus lamiiformis* Nees (lectotype, here selected).

Flowers sessile or shortly pedunculate in the axils of the upper leaves, bibracteolate, generally solitary, sometimes in fascicles. Calyx segments narrow, united in the base, the posterior longer. Capsule obovate in contour, apiculate, with a narrow solid base ⅓ its length. Seeds 6–8.

Species of this group are characterized by their sharply quadrangular stems, frequently reduced axillary cymes, and few-seeded capsules. They are common in floristic provinces of the Amazon region or dominion (see Cabrera & Willink, 1980), at low elevations, growing in moist soil.

The name of this infrageneric group together with *Calycosi*, *Genuini*, *Inaequifolii*, *Paniculati*, and *Subspicati* were proposed by Nees (1847a, b) under *Dipteracanthus*, but without a clear indication of rank. Following article 35 of the *International Code of Botanical Nomenclature* (Greuter et al., 1988), these names are valid provided that all other requirements for valid publication are fulfilled, and may act as homonyms or serve as basionyms for subsequent combinations in definite ranks.

**12. Ruellia epallocaulos** Leonard ex Ezcurra & Wasshausen, Brittonia 44(1): 69. 1992. TYPE: Paraguay. In regione fluminis Alto Paraná, *Fiebrig 5372* (holotype, SI; isotypes, G, GH, K, LIL, US). Figure 16.

Suffruticose perennial 0.30–1 m tall, branched from a subligneous base. Stems erect or somewhat decumbent, quadrangular, glabrous, rooting at the nodes. Leaves on glabrous petioles 0.4–1 cm long, the blade ovate, 3–6(–10) cm long and 1–2(–3.5) cm wide, acute or acuminate, obtuse or rounded at the base, glabrous, the margins faintly and irregularly crenate. Flowers sessile, solitary, sometimes in twos, in reduced subsessile dichasia condensed in the axils of the upper leaves, exceptionally pedunculate. Bracteoles small, lanceolate, 3–5 mm long. Calyx 1–1.8 cm long, the segments oblong-lanceolate, rounded or obtuse, to 1.5 cm long, ± glabrous, shortly ciliate, the posterior longest. Corolla purple or blue, 4–5 cm long, the basal tube 1.8–2.5 cm long, the throat obconic, 1–1.5 cm long and ca. 1.2 cm diam., the lobes spreading, suborbicular, 0.5–1 cm wide. Stamens included,

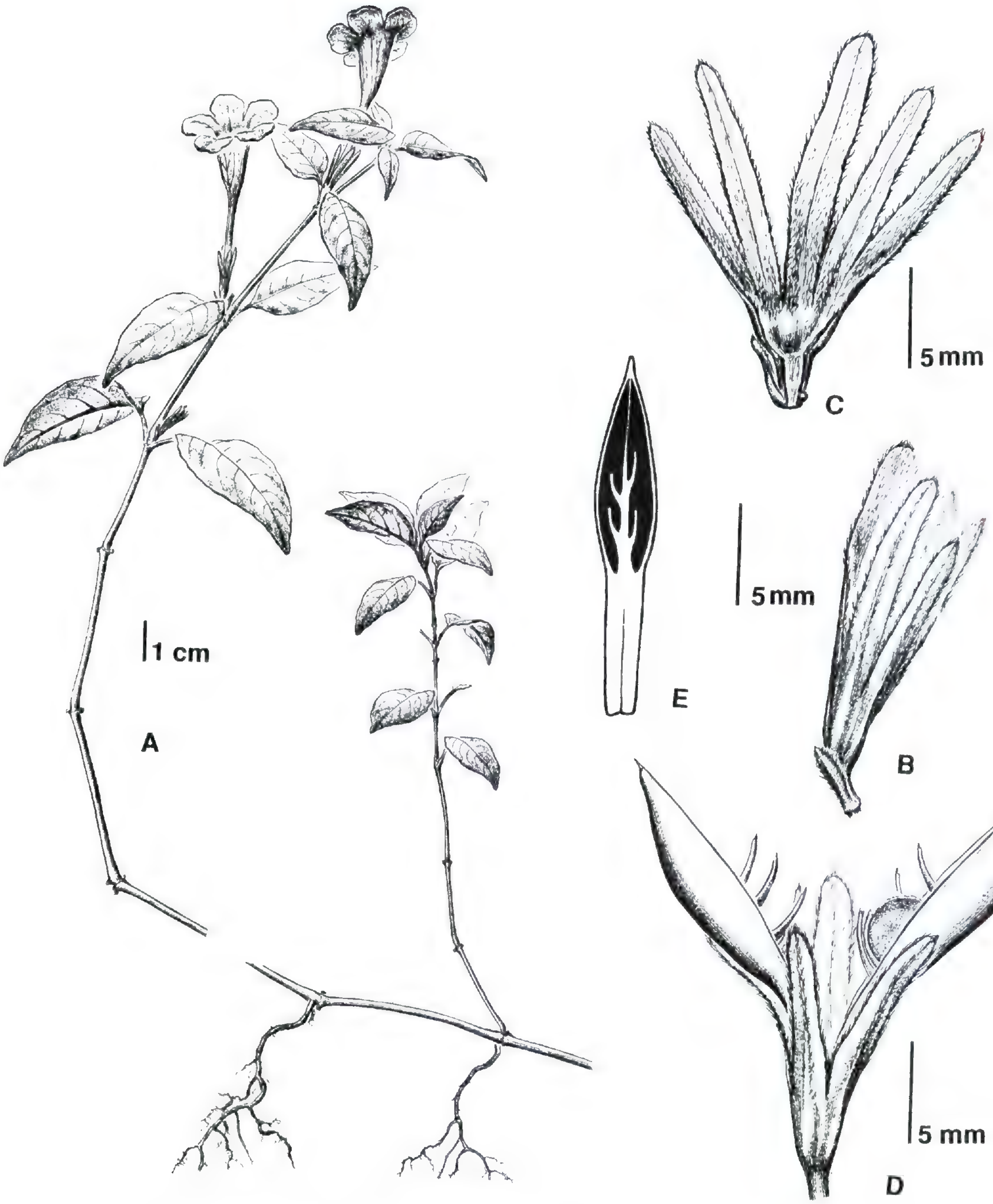


FIGURE 16. *Ruellia epallocaulos* Leonard ex Ezcurra & Wasshausen.—A. Habit.—B. Calyx with bracteoles.—C. Open calyx.—D. Dehiscent capsule.—E. Open capsule without seeds, schematic. (A–E, *Hatschbach 8322.*)

long filaments ca. 8 mm long, short 6 mm long, the anthers 2.5 mm long. Ovary and style glabrous. Capsule narrowly ovate, 1.2–1.5 cm long and 3–4 mm thick, slightly apiculate, with a solid base ca. 4 mm long, the surface glabrous. Retinacula 2 mm long; seeds 6–8, 2–2.5 mm diam., glabrous, the margins pubescent and mucilaginous when wet.

*Distribution.* Eastern Paraguay, northeastern Argentina, and southern Brazil, on the basin of the Paraná River (Paranaense phytogeographical province). It is found in the shade of the gallery forest, generally in humid places near watercourses. It flowers in spring, from August to October.

*Representative specimens.* ARGENTINA. **Misiones:** Yarupá, Arroyo Las Tranqueras, *Grondona &*

*Spegazzini 1374* (BAB); Puerto Pampa, *Kermes 197* (BAB); San Ignacio, *Quiroga s.n.* (BA 21419); Depto. Montecarlo, Arroyo Piray Guazú y ruta 12, *Schinini 19904* (CTES). BRAZIL. **Paraná:** Mun. Cerro Azul, Turvo, *Hatschbach 5025* (MBM); Mun. Cerro Azul, Cerro Azul, *Hatschbach 8322* (HBR, MBM, US); Mun. Cianorte, Fazenda Lagoa, *Hatschbach 16950* (MBM, US); Mun. Cerro Azul, Barra do Tigre, *Hatschbach 40347* (MBM, US). PARAGUAY. **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 5751* (G, SI); Reserva Itabó, *Itaipú Binacional 925* (MO).

*Ruellia epallocaulos* is characterized by the relatively large, solitary, bluish flowers and the markedly quadrangular stems. It is sometimes confused with the sympatric, red-flowered *Ruellia angustiflora*, because of its similar habit.

**13. Ruellia kleinii** Ezcurra & Wasshausen, Brittonia 44(1): 72. 1992. TYPE: Brazil. Santa Catarina: Florianópolis, Morro de Riberão, *Klein 7333* (holotype, US; isotypes, HBR, MBM). Figure 17.

Small suffruticose herb to 50 cm high; stems erect, markedly quadrangular. Leaves ovate, 2.5–3.3 cm long, 1.5 cm wide, acute and acuminate, cuneate, puberulous. Flowers subsessile, solitary, sometimes in sessile or pedunculate dichasia reduced to 3 flowers or less, in the axils of the upper leaves; bractlets foliaceous, less than 1 cm long and 3–4 mm broad. Calyx ca. 1 cm long, with linear segments 7–8 mm long and 1 mm broad, puberulous. Corolla white, 1.5–2 cm long, the basal tube 6–7 mm long, the throat obconic, 6 mm long, 5 mm diam., the lobes suberect, 4 mm long and 3 mm broad. Stamens included, long filaments 4 mm long, short 3 mm long, the anthers ca. 1.5 mm long. Capsule markedly stipitate, ca. 1 cm long, apiculate, few-seeded.

*Distribution.* Southern Brazil, in openings in forests, frequently on wet ground along watercourses.

*Representative specimens.* BRAZIL. **Santa Catarina:** Ilha de Santa Catarina, Florianópolis, no pasto úmido, *Klein & Bresolin 8476* (US); Ilha de Santa Catarina, Tapera, Ribeirão, orla da mata, *Klein & Bresolin 8532* (US); Ilha de Santa Catarina, Florianópolis, Lagoa do Piri, *Klein & Souza 8626* (US), *Smith & Reitz 6192* (US).

*Ruellia kleinii* is characterized by the delicate, quadrangular stems and the small flowers with ovate bracteoles. It is quite similar to some of the specimens included by Nees in the original description of *Dipteracanthus menthoides* Nees, but has smaller, ovate leaves and is found in a more southern area.

## IV. Group **Dipteracanthus**

*Ruellia* L. sect. *Dipteracanthus* (Nees) Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 309. 1895.

*Dipteracanthus* Nees in Wallich, Pl. Asiat. Rar. 3: 81. 1832. TYPE: *Dipteracanthus prostratus* Nees.

*Gymnacanthus* Nees in Lindl., Nat. Syst. Bot. ed. 2: 444. 1836, not Oersted, 1854. TYPE: *Gymnacanthus petiolaris* Nees.

*Dipteracanthus* (*Calycosi*) Nees in DC., Prodr. 11: 116. 1847.

*Dipteracanthus* Nees (*Genuini*: *Bracteolati*) Nees in DC., Prodr. 11: 117. 1847.

*Siphonacanthus* Nees in C. Martius, Fl. Bras. 9: 45. 1847. TYPE: *Siphonacanthus villosus* Nees.

Flowers sessile, solitary, borne in the axils of the upper leaves, bibracteolate. Capsules thick, oblong in contour, with a small solid base ¼ their length. Seeds 6–12.

Group *Dipteracanthus* is pantropical and possibly the one with the most species in the genus. The neotropical species have been separated from the Old World *Dipteracanthus* by Bremekamp (1969: 423), but the characters that supposedly differentiate them are inconsistent. Taxonomically, it is the most problematic group; in southern South America it is partly represented by the assemblage of species allied to *Ruellia dissitifolia*, which are very difficult to delimit. Most of these species are suffruticose herbs that grown in open areas of floristic provinces of Amazon region or dominion (see Cabrera & Willink, 1980).

**14. Ruellia brachysiphon** (Nees) Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4, Abt. 3b: 310. 1895. *Dipteracanthus brachysiphon* Nees in C. Martius, Fl. Bras. 7: 34. 1847. TYPE: Brazil. Rio Grande do Sul: Porto Allegre, *Sellow 68* (holotype, B destroyed, photo F 5911; isotype, K).

Erect herb to 30 cm tall, with stems subterete, ± branched, velutinous, arising from a small rhizome. Leaves shortly petiolate, the blades elliptic to widely ovate, 2–4 cm long, 1.5–3 cm wide, acute, obtuse or rounded at the apex, sometimes apiculate, cuneate at the base, ± entire, sometimes serrulate, the lower ones smaller and rounder, all softly and shortly velutine-puberulous to densely velutinous, with some hairs glandular, sometimes glutinose, the underside densely pale velutinous.

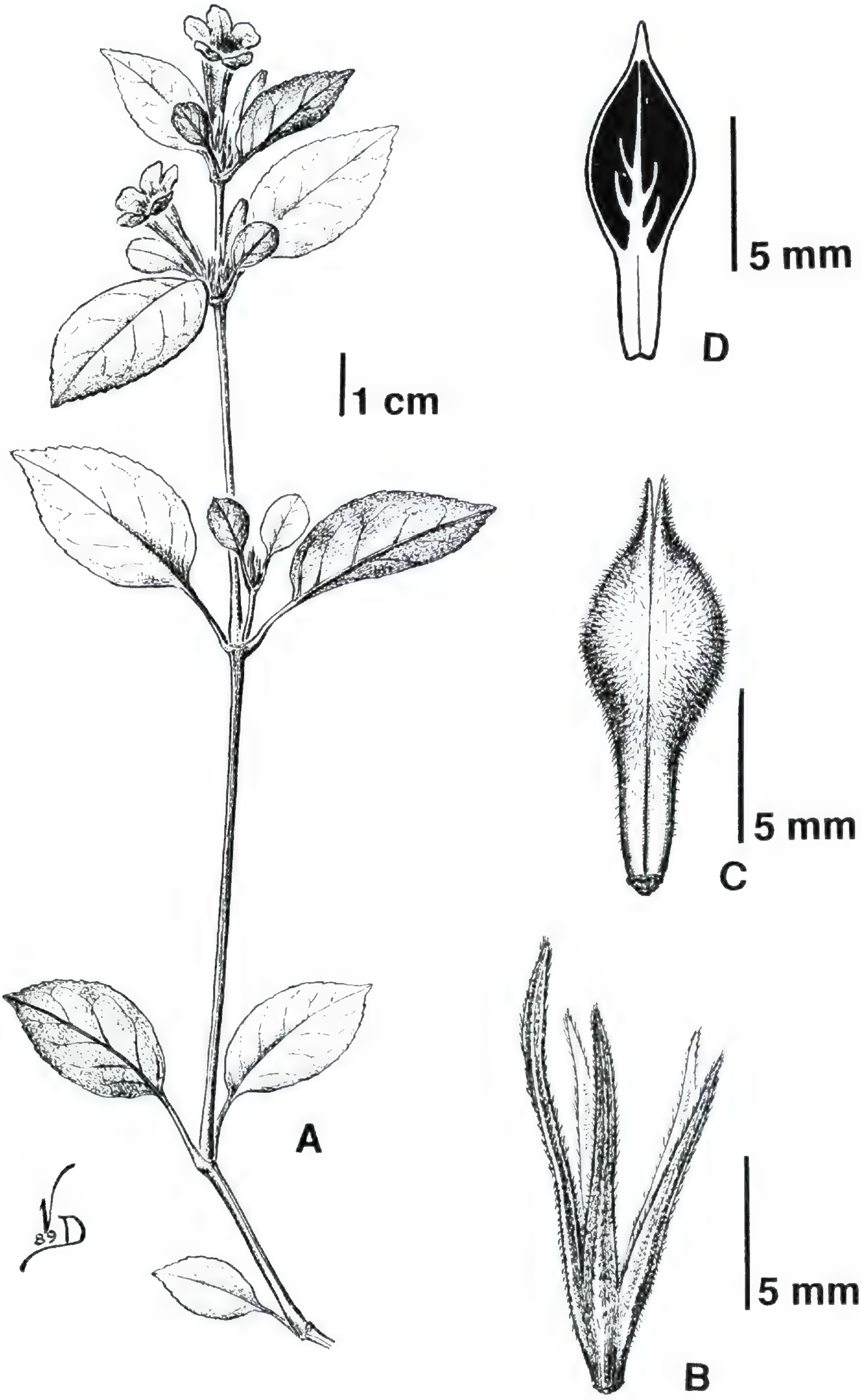


FIGURE 17. *Ruellia kleinii* Ezcurra & Wasshausen.—A. Flowering branch.—B. Calyx.—C. Capsule.—D. Open capsule without seeds, schematic. (A–C, *Klein 7333*; D, *Klein & Bresolin 8476*.)

Flowers sessile, solitary in the axils of the terminal leaves. Bractlets elliptic or lanceolate, ca. 1.5 cm long and 3–5 mm wide, acute, foliaceous, densely pubescent. Calyx 1–2 cm long, the segments ovate or lanceolate, to 1.5 cm long and 2–7 mm wide, acute, shortly puberulent to densely pubescent or velutinous, ciliate. Corolla erect, pale blue, 4–5 (–8) cm long, the basal tube less than 1(–2) cm long, the throat 2–2.5(–4) cm long, and 1.5(–2) cm wide, the lobes spreading, suborbicular, 1–1.5(–2) cm wide. Stamens included, long filaments ca. 1 cm long, short 0.5 cm long, the anthers 3 mm long. Mature capsule unknown.

*Distribution.* Eastern Paraguay, northeastern Argentina, and southern Brazil; occurring rarely in open, high campos, and flowering in spring, from September to December.

*Representative specimens.* ARGENTINA. **Corrientes:** Virasoro, *Birabén 5054* (LP); Desiderio Sosa, *Birabén 5211* (LP); Ituzaingó, sobre ruta 12, próximo al límite con Misiones, *Legname 8627, 8637* (LIL). **Misiones:** Entre Pueblo Santa Ana y cerro Santa Ana, *Alboff*, 26 Nov. 1896 (LP); Depto. Candelaria, Loreto, *Montes 32* (LP), *840* (BAB, LP); Depto. Iguazú, Puerto Esperanza, *Montes 9458* (LIL); Depto. Iguazú, Puerto Wanda, *Montes 10409* (LP); Depto. Iguazú, El Dorado, *Schmidt 2776* (LIL, pro parte); Depto. San Ignacio, Pastoreo, Arroyo Las Tunas, *Schmidt 5036* (LIL); Santa Ana, Misiones, *Spegazzini s.n.*, Jan. 1907 (LP). BRAZIL. **Paraná:** Ponta Grossa, campos altos, *Hoehne*, 1 Nov. 1928 (SP). **Rio Grande do Sul:** Canoas, *Augusto*, 20 Feb. 1943 (ICN). PARAGUAY. **Alto Paraná:** Irala, *Montes 9912* (LIL). **Caaguazú:** in campis, *Hassler 9225* (G); 15 km N de Caaguazú, amino a lhú, *Schinini 21977* (CTES).

*Ruellia brachysiphon* is a problematic species, variable in calyx morphology, and with a wide distribution, although apparently represented only by a relatively small number of specimens. It is characterized by the corollas with a short basal tube, the frequently wide calyx lobes, and the velutine-puberulous surface of the leaves.

**15. Ruellia brevicaulis** (Nees) Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4, Abt. 3b: 310. 1895. *Dipteracanthus brevicaulis* Nees in C. Martius, Fl. Bras. 7: 35. 1847. TYPE: Brazil. Without locality, *Sellow 3190* (holotype, B destroyed, photo F 5912). Figure 18.

*Dipteracanthus dissitifolius* Nees var. *humilior* Nees in C. Martius, Fl. Bras. 9: 35. 1847. SYNTYPES: Brazil. Minas Gerais: *Claussen 232* (P not seen); São Paulo: São Paulo, *Lund 733* (G not seen, photo herb. DC); Without state: Puerto Grosso, *Sellow s.n.* (B destroyed, photo F 5919). Syn. nov.

Erect, suffruticose herb, the stems terete, to 30 cm long, hirsute, arising from a small woody rhizome with thick, fleshy, fusiform roots. Leaves on petioles to 0.3 cm long, the blades widely ovate, 3–5 cm long and 1.5–3 cm wide, acute at the apex, cuneate at the base, serrulate, the lower ones generally smaller, all hirsute-pilose, the hairs long, white, shiny and spreading, sometimes also mixed with short, sericeous pubescence. Flowers sessile, solitary in the axils of the terminal leaves. Bractlets oblong, foliaceous, 1.5 cm long and 2–5 mm wide, acute, long-pilose. Calyx 1.5–2 cm long, the segments linear-lanceolate, to 1.8 cm long and 2 mm wide, acute, hirsute-ciliate. Corolla pale blue, 5–7 cm long, the basal tube 1–2 cm long, the throat longer, obconic, to 4 cm long and 2.5 cm diam., the lobes speading, suborbicular, ca. 2 cm wide. Stamens included, long filaments ca. 1 cm long, short 0.5 cm long, the anthers 3 mm long. Ovary and style glabrous. Capsule oblong in shape, 1.2–1.5 cm long and 0.5 cm thick, with a solid base ⅛ its length, the surface puberulous. Retinacula 3 mm long; seeds 6–8, lenticular, 3–4 mm diam., with margins appressed-puberulous, densely mucilaginous when wet.

*Distribution.* Southern Brazil, northeastern Argentina, and eastern Paraguay. *Ruellia brevicaulis* is common in open, high campos, to 950 m, especially on rocky or sandy ground subject to periodic fires. It flowers in spring, from September to December.

*Representative specimens.* ARGENTINA. **Corrientes:** Depto. Santo Tomé, Arroyo Chirimay, *Correa 6852* (BAB); Ruta 14, Gobernador Virasoro, *Krapovickas 16710* (CTES); 15 km de Virasoro camino a Garruchos, *Krapovickas 20961* (CTES); Santo Tomé, Estancia Garruchos, casco, *Krapovickas 21436* (CTES); Depto. Ituzaingó, Estancia Puerto Valle, *Partridge s.n.*, (BA 61610); Depto. Ituzaingó, Estancia Rincón Chico, *Tressens 342* (CTES). **Misiones:** Depto. San Pedro, Campo Cumprido, *Bertoni 2097* (LIL, US); Apóstoles, Escuela Agrotécnica, *Cabrera 28593* (SI); Santa Ana, *de Llamas 621* (BAB); 30 km de L. N. Alem, camino a San Javier, sobre ruta 4, *Krapovickas 15200* (CTES); Loreto, *Montes 59, 248, 684* (all LP); Santo Pipó, *Grondona & Piccinini 3215* (BAB); San Ignacio, Naucauguazú, *Schwarz 5021* (LIL, US). BRAZIL. **Paraná:** Estrada de Curitiba a Ponta Grossa, *Dombrowski 2023* (PKDC); Palmeira, Fazenda Santa Rita, *Dombrowski 12077* (PKDC); Curitiba, in campo, *Dusén 17277* (GH); Mun. Curitiba, Cajurú, *Hatschbach 392* (MBM); Mun. Lapa, Rio Passa Dois, *Hatschbach 6419* (LIL, MBM, US); Mun. São Jose dos Pinhais, Campo Largo de Roseira, *Hatschbach 8338* (MBM, US); Mun. Ponta Grossa, Parque Vila Velha, *Hatschbach 45470* (MBM); Mun. Curitiba, Capanema, *Kumrow 2364* (MBM, US); Curitiba, Cidade Industrial, *Pedersen 10885* (CTES); Araucaria, *Pereira*

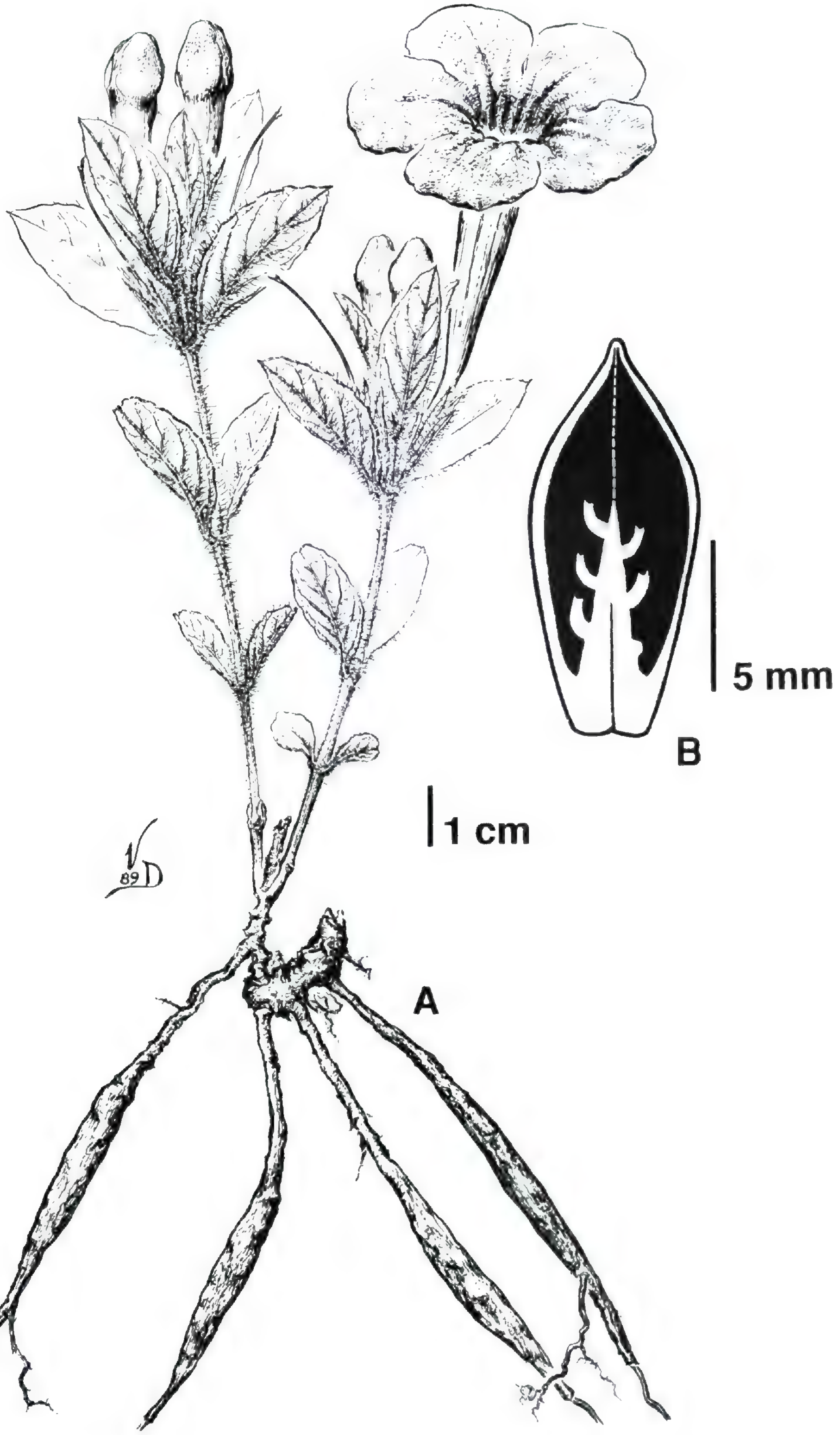


FIGURE 18. *Ruellia brevicaulis* (Nees) Lindau.—A. Habit.—B. Open capsule without seeds, schematic. (A, *Partridge s.n., BA 61609*; B, *Cabrera 28593.*)

*8084* (RB). **Rio Grande do Sul:** Tres Barras, in pseudo campo, *Dusén 17610* (GH); Arroio Tatim, Soledade, *Fleig 194, 205* (ICN); 27 km N de Vacaría, BR 116, km 258, *Krapovickas & Vanni 36860* (CTES, US); Santa María, *Lindeman 8259* (ICN); Esmeralda, Estação Ecológica Aracuri, *Miotto 983* (ICN); Pinhal, *Palacios & Cuezzo 2358* (LIL); Passo do Socorro, p. Vacaria, *Rambo 51597* (HBR, US); Esteio, prope Porto Alegre, *Rambo 57168* (HBR, US). **Santa Catarina:** Curitibanos, Ponte Alta do Sul, *Klein 3246* (HBR, US); Curitibanos, campo, *Klein 4068* (HBR, US); Lajes, Passo do Socôrro, *Klein 4423* (HBR, US); Lajes, Morro do Pinheiro Sêco, *Klein 4529* (HBR, US); Campos Novos, campo, *Reitz & Klein 14296* (HBR, US); Abelardo Luz, *Reitz & Klein 16509* (HBR, US); ao longo da Estrada de Rodagem Federal ao sul de Lajes, *Smith & Klein 8117* (HBR, US); Fazenda Esperança, Campos de Palmas, 6 km ao sul de Horizonte, *Smith & Klein 13494* (HBR, US); 8 km ao oeste de Campo Erê, *Smith & Klein 13782* (HBR, R, US). PARAGUAY. **Amambay:** N Paraguay, zwischen Río Apa und Río Aquidabán, *Fiebrig 4378* (BM). **Cordillera:** Prairies de Capitindú à l'E de la Cordillère de Villa Rica, *Balansa 2462* (P); Doña Juana, près de Villa Rica, *Balansa 2462a* (K, P). **Alto Paraná:** Irala, *Montes 9912* (LIL). **Caazapá:** Distrito Yuty, 20 km E de San Miguel, desvío a 3 de Mayo y Capituidy, *Arbo 2889* (CES). **Canendiyú:** In regione yerbalium de Maracayú, *Hassler 4281* (BM). **Misiones:** Ruta 4, 20 km E de San Ignacio, *Schinini 21941* (LIL).

*Ruellia brevicaulis* is characterized by the fusiform, tuberous roots, the hirsute pilosity—the hairs long, shiny and spreading—and the large, blue corollas with a short basal tube and a large throat. It is a common species in open, elevated campos of southern South America subject to periodic fires. The epithet "brevicaulis" is well applied to specimens of plants that have recently been burnt and only produce short stems before flowering. Some specimens do produce longer stems, probably when fires are less frequent.

Specimens of *Ruellia brevicaulis* have often been misidentified as *Ruellia dissitifolia* (e.g., Wasshausen & Smith, 1969), but *R. dissitifolia* is a different species only found in central Brazil (Goiás, Minas Gerais, and São Paulo), characterized by the basal obovate leaves, the dense, whitish, velutino-sericeous pubescence, and the large flowers.

*Ruellia brevicaulis* seems to hybridize with *Ruellia coerulea*, a species of group *Ruellia*, as suggested by the existence of morphologically intermediate specimens from eastern Paraguay, where both species are sympatric (see description of *R. coerulea*).

**16. Ruellia multifolia** (Nees) Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 310. 1895. *Dipteracanthus multifolius* Nees in C. Martius, Fl. Bras. 7: 33. 1847. SYNTYPE: Brazil. *Sellow s.n.* (syntype, B destroyed, photo F 5938; isosyntype, K). Figure 19.

Erect herb or suffruticose perennial to 35 cm high, with stems subterete, ± branched, velutinous or hirsute on some sectors, arising from a horizontal rhizome with numerous, thick, fusiform roots. Leaves subsessile or shortly petiolate, the blades elliptic to widely ovate, 2–5 cm long, 1.5–3 cm wide, acute, obtuse or rounded at the apex, sometimes apiculate, cuneate or truncate at the base, ± entire, sometimes serrulate, the lower ones smaller and rounder, all softly and shortly velutine-puberulous to densely hirsute-velutinous, with many glandular hairs, sometimes glutinose, the underside with ± densely scattered sessile patelliform glands. Flowers sessile, solitary in the axils of the terminal leaves. Bractlets elliptic or lanceolate, foliaceous, ca. 1.5 cm long and 3–4 mm wide, acute, foliaceous, densely glandular-pubescent to shortly velutinous. Calyx 1–2 cm long, the segments lanceolate, to 1.5 cm long and 2 mm wide, acute, glandular-pubescent or velutinous, ciliolate. Corolla erect, pale mauve, 4–7 cm long, the basal tube 1.5–3 cm long, the throat 1.5–3 cm long and 1.5–2 cm wide, the lobes spreading, orbicular, 1.5–2 cm wide. Stamens included, long filaments ca. 1 cm long, short filaments 0.5 cm long, anthers 3 mm long. Style ± glabrous. Capsule oblong 1.5–1.8 cm long and ca. 5 mm thick, with a solid base ⅛ its length, the surface glabrous. Retinacula 3 mm long; seeds 6–12, 3 mm diam., with margins appressed-puberulous.

*Distribution.* Central and southern Brazil, eastern Paraguay, and northeastern Argentina. It is found growing in open cerrado and elevated campos, frequently on sandy soil. It flowers in spring and summer, from October to March.

**16a. Ruellia multifolia** (Nees) Lindau var. **multifolia.** Figure 19A.

This variety is characterized by the somewhat suffruticose habit, the generally unbranched stems, the densely velutinous-hirsute elliptic leaves that turn glabrescent on the upper surface at maturity, and the coriaceous blade with the nerves prominent below.

*Distribution.* Northeastern Argentina, eastern Paraguay, and central and southern Brazil.

*Representative specimens.* ARGENTINA. **Misiones:** Campo Grande, km 184, *Bertoni 623* (LIL); Depto. San Ignacio, Jardín América, *Crisci 324* (LP); San Ignacio, campo alto arenoso, *Quiroga 381* (BA); Santa Ana, *Rodríguez 769* (BA, LIL); San Ignacio, *Schulz*

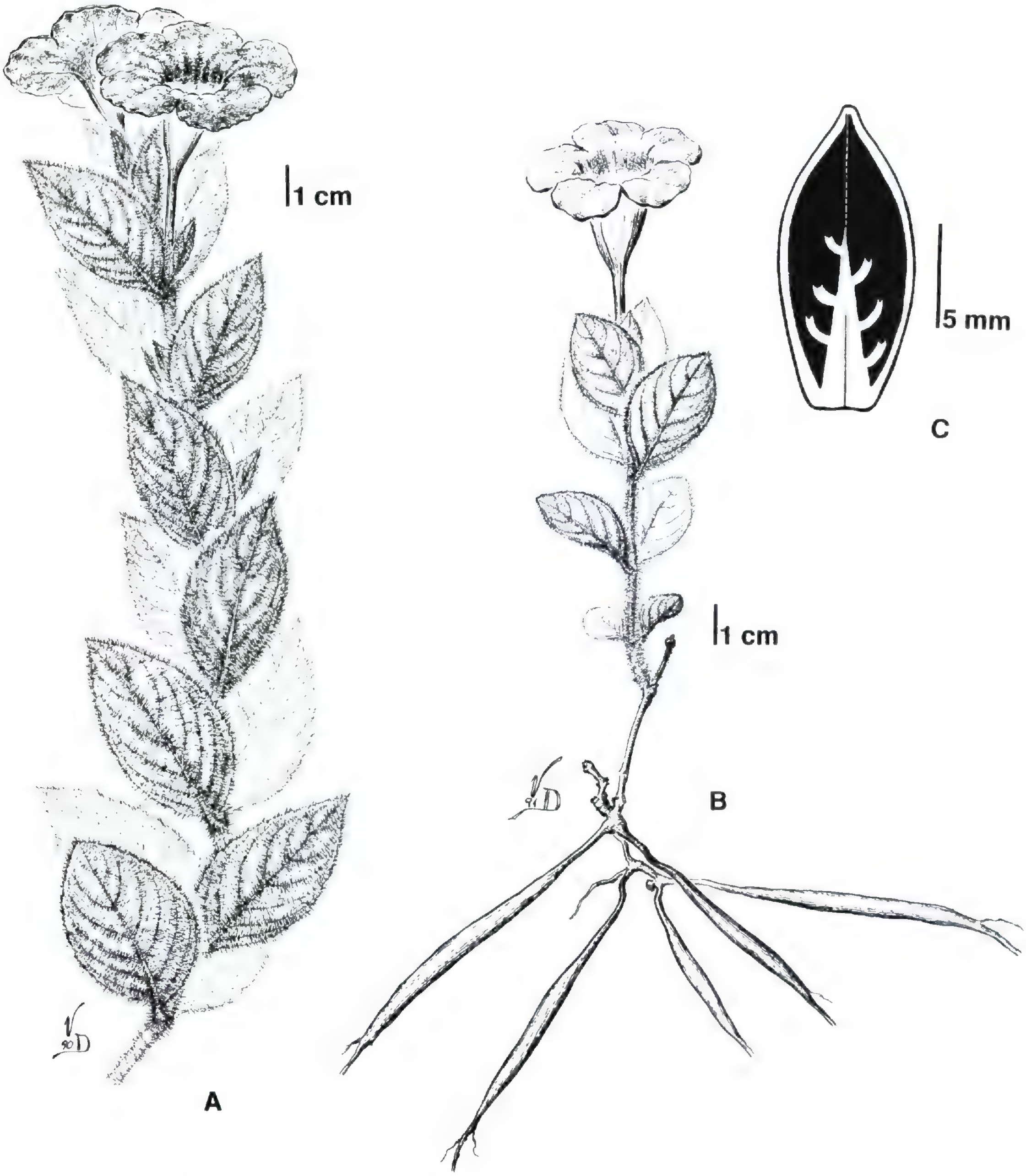


FIGURE 19. *Ruellia multifolia* (Nees) Lindau.—A. Flowering branch of *R. multifolia* var. *multifolia*.—B. Habit of *R. multifolia* var. *viscossisima* (Nees) Ezcurra.—C. Open capsule without seeds of variety *multifolia*, schematic. (A, *Hassler 1804*; B, *Krapovickas & Cristobal 13618*; C, *Zuloaga 3276*.)

*7113* (LIL); De San Ignacio a Santa Ana, a 6 km de San Ignacio, *Zuloaga 3299* (SI); Apóstoles, Escuela Agrotécnica Pascual Gentilini, *Zuloaga 3276* (SI). BRAZIL. **Paraná:** Castro, en campo, *Dombrowski 11994* (HBR); Campo Mourão, *Hatschbach 7621* (MBM); Arapoti, Rio das Cinzas, barra do Perdizes, *Hatschbach 8563* (MBM); Mun. Senges, Rio Pelame, *Hatschbach 26786* (MBM, US). **Santa Catarina:** Campo Erê, Fazenda São Vicente, *Klein 4999* (HBR), *Smith & Klein 11550* (HBR, RB, US); Campo Erê, Chapecó, *Reitz 4499* (HBR, NY, US); Campo Erê, *Smith & Reitz 9373* (US). PARAGUAY. **Alto Paraná:** Reserve Tajijupi, Hernandarias 6 km, *Stutz 2133* (G). **Amambay:** zwischen Río Apa und Río Aquidaban, *Fiebrig 4423* (G); Cursus superioris fluminis Apa, *Hassler 8009* (G); Parque Nacional Cerro Corá, cerrado camino a Lorito Picado, *Soria & Ortiz 4196* (MO). **Caaguazú:** Caaguazú, cerca y al sur de Ihú, *Fernández Casas & Molero 6438* (G, MO, NY). **Caazapá:** propiedad del Señor Trosiu, *Ortiz 1091* (G). **Canendiyú:** Sierra de Maracayú, *Hassler 5092* (G, GH, NY pro parte); in campo prope Igatimí, *Hassler 5648* (G). **Concepción:** zwischen Río Apa und Río Aquidabán, Cen-

turión, *Fiebrig 4378* (G, K). **Cordillera:** Cordillera de Altos, *Fiebrig 374* (G), *Hassler 1804* (G, US); in campo Itacurubi, *Hassler 1704* (G); in campis Tobaty, *Hassler 3259* (G, GH, NY, P); In valle fluminis Y-hacá, in campo prope Piribebuy, *Hassler 6814* (G); Arroyo Y-hacá guazú, *Schwarz 11226* (LIL); Valenzuela, Río Y-hacá, *Sparre & Vervoorst 1158* (LIL). **Guairá:** Villa Rica, *Jorgensen 4307* (LP, MO, US). **Paraguarí:** Parque Nacional Ybicuí, campo cerrado 5 km N of administration building on road to Cesar Barrientos, *Zardini 8698* (MO). **San Pedro:** in regione vicine San Estanislao, *Hassler 4278* (G); in regione fluminis Tapiraguay, *Hassler 5973* (G).

**16b. Ruellia multifolia** (Nees) Lindau var. **viscossisima** (Nees) Ezcurra, stat. nov. *Dipteracanthus viscossisimus* Nees in C. Martius, Fl. Bras. 9: 34. 1847. *Ruellia viscossisima* (Nees) Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4, Abt. 3b: 310. 1895. TYPE: Brazil. Without locality: *Sellow 1413* (holotype, B destroyed, photo F 5960; isotype, K). Figure 19B.

*Dipteracanthus glanduloso-punctatus* Nees in C. Martius, Fl. Bras. 9: 34. 1847. *Ruellia glanduloso-punctata* (Nees) Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4, Abt. 3b: 310. 1895. SYNTYPE: Brazil. "Rio Grande do Sul": S. Ignacio, *Sellow s.n.* (B destroyed, photo F 5924). Syn. nov.

This variety differs from *Ruellia multifolia* var. *multifolia* by the more herbaceous habit, the less branched stems, the widely ovate leaves, obtuse or rounded at the apex, the shortly and softly velutinous pubescence with many glandular hairs, frequently glutinose, the underside with densely scattered sessile patelliform glands.

*Distribution.* Southeastern Paraguay and limiting areas of northeastern Argentina and southern Brazil, in campos.

*Representative specimens.* ARGENTINA. **Corrientes:** Depto. Mburucuyá, Estancia Santa Teresa, *Burkart 19512* (SI); Depto. Mburucuyá, 10 km W de Mburucuyá, *Krapovickas & Cristóbal 13618* (CTES, LP, US); Depto. Mburucuyá, Estancia Santa Teresa, *Pedersen 2995* (AA); Depto. San Miguel, 21 km S de Loreto, *Schinini 8202* (CTES). **Misiones:** Posadas, Loreto, *Ekman 910* (US); San Ignacio, casa de Horacio Quiroga, *Krapovickas & Cristóbal 28729* (US). PARAGUAY. **Alto Paraná:** Reserva Itatí Yupí, *Itaipú Binacional 170* (MO). **Caaguazú:** Caaguazú dans les campos, *Balansa 2462b* (P). **Caazapá:** Tavaí, propiedad de la familia Bogado, *Basualdo 2140* (MO); Tavaí, 3 km S del Destacamento, *Soria 3275* (MO). **Concepción:** in regione superioribus cursus fluminis Apa, *Hassler 8009* (G). **Cordillera:** in campo prope Itacurubí, *Hassler 1704* (P); in dumeto Cordillera de Altos, *Hassler 3500* (G). **Without locality:** Paraguaria centralis, *Hassler 3529* (BM, P, NY); en el campo Irupé, *Jorgensen 4307* (SI).

*Ruellia multifolia* var. *viscossisima* is closely related morphologically to *Ruellia multifolia* var. *multifolia*, with which it can often be confused. Variety *multifolia* is a generally more robust form that is quite frequent in south-central Brazil and northeastern Paraguay. Variety *viscossisima*, more common in southeastern Paraguay and limiting areas of northeastern Argentina, may just be a herbaceous, short-lived form, the product of seasonal climatic factors associated with latitude, such as photoperiod and temperature, or of edaphic conditions.

Although this variety was described from material reported to have been collected by Sellow in southern Brazil (Nees, 1847a: as *Dipteracanthus viscosissimus* and *D. glanduloso-punctatus*), I have found no other Brazilian material of this plant. The Spanish name of the only locality that appears in the type specimens ("S. Ignacio," and not the Portuguese orthography "S. Inácio") suggests that this material could have also been collected in northeastern Argentina near Brazil, in San Ignacio, Misiones, where the plant has been found relatively recently.

**17. Ruellia solitaria** Vell. Conc., Fl. Flumin.: 266. 1829. TYPE: Brazil. Rio de Janeiro: illustrated in Fl. Flumin. Icon. 6: t. 95. 1831. Figure 20.

*Dipteracanthus schauerianus* Nees, Ind. Sem. Hort. Vratisl. 1832 (not seen). Linnaea 16: 290. 1842. TYPE: "Col. in Cald." (not seen).

*Dipteracanthus calvescens* Nees in C. Martius, Fl. Bras. 9: 32. 1847. *Ruellia calvescens* (Nees) Lindau in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 310. 1895. SYNTYPES: Brazil. Rio de Janeiro: Lacané, July 1839, *Gardner 805* (K; isosyntype, BM); Sebastianopolim, *Martius s.n.* (M, photo SI); Corcovado, *Riedel s.n.* (LE not seen); without locality, *Schott 6129* (W not seen, photo F 32759), *Sellow s.n.* (B destroyed, photo F 5913).

Branched, suffruticose herb 30–50 cm tall. Stems erect, obscurely quadrangular, pale whitish and terete at maturity, glabrous. Leaves on petioles 0.5–1 cm long, the blades widely elliptic or ovate, 5–12 cm long and 2–4 cm wide, obtuse or rounded at the base, glabrous on the surface, the margins entire. Flowers sessile, solitary in axils of the upper leaves, sometimes in twos. Bracteoles ovate, foliaceous, 1.5–2.5 cm long and 0.5–0.8 cm wide, glabrous. Calyx 0.8–1 cm long, the segments linear, to 0.8 cm long and 2 mm wide, acute, glabrous, ciliolate, somewhat accrescent and remaining on the stems after the shedding of the capsules. Corolla white or pale mauve, ca. 5 cm long, the basal tube 2 cm long, the throat obconic, 2.5 cm long and 1.3 cm diam., the lobes spreading, suborbicular, 1.3–1.8 cm wide. Stamens included, long filaments

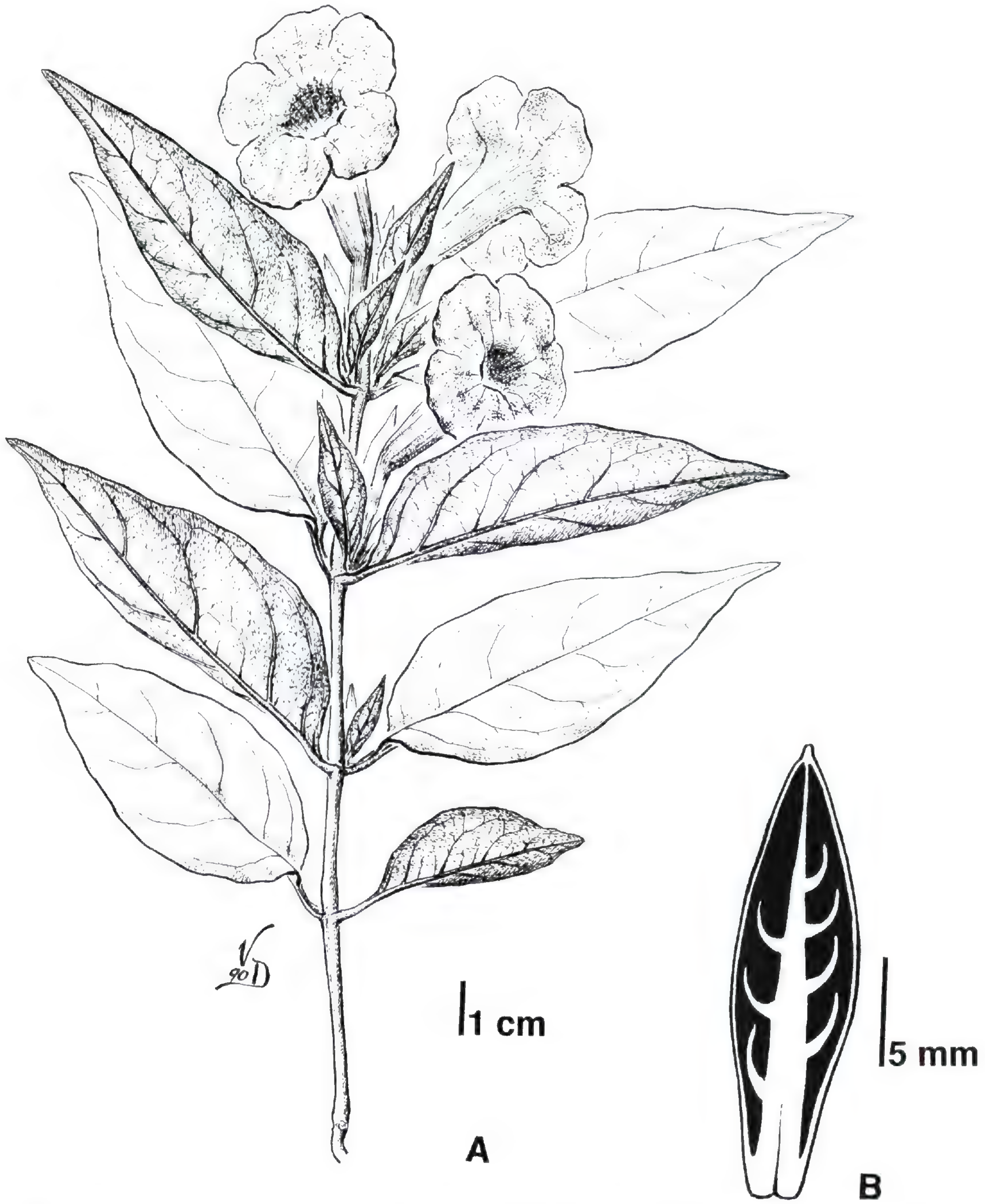


FIGURE 20. *Ruellia solitaria* Vell.—A. Flowering branch.—B. Open capsule without seeds, schematic. (A, *Hatschbach 34793*; B, *Hatschbach 14708*.)

ca. 1.2 mm long, short 0.8 mm long, the anthers 3 mm long. Ovary and style glabrous. Capsule oblong-ovate, 1.5–2 cm long and 5 mm thick, with a short solid base 3–5 mm long, the surface glabrous. Retinacula 2 mm long; seeds 12–16, 2 mm diam., glabrous, the margins pubescent and mucilaginous when wet.

*Distribution.* Southern Brazil, in the hygrophilous forest on the eastern side of the southeastern Atlantic coastal ranges, from the states of Espírito Santo and Rio de Janeiro to Paraná ("Mata Atlantica," Atlántica floristic province). It is found in the shady underwood of the forests. It flowers in winter and spring, from July to October.

*Representative specimens.* BRAZIL. **Paraná:** Mun. Morretes, Formigueiro, *Hatschbach 345* (MBM, RB); Grota Funda, *Hatschbach 4068* (MBM); Morro 7 encosta occidental, *Hatschbach 11340* (MBM); Estrada Itupava, Rio São João, *Hatschbach 14708* (MBM, NY, US); Estrada da Graciosa, Ferradura, *Hatschbach 19237* (MBM); Mun. Morretes, Estrada Graciosa, Grota Funda, *Hatschbach 34793* (MBM, US); Rio Bromado, *Hatschbach 42499* (MBM); Rio Taquaral, *Hatschbach 44983* (MBM, US); Mun. Campina Grande do Sul, Serra Capivari Grande, *Hatschbach 16209* (MBM, US). Mun. Guaraqueçaba, Rio do Cedro, *Hatschbach 19237* (MBM).

*Ruellia solitaria* is characterized by the glabrous stems and leaves, and the large, white or pale mauve, sessile, solitary flowers, with a pair of widely ovate bracteoles in the base. It is frequent in the understory of the coastal hygrophilous forest of southeastern Brazil. It is similar to *Ruellia lilacina* Hooker, a blue-flowered species of Amazonian Peru.

## V. Group **Ebracteolati**

*Dipteracanthus* Nees (Genuini: *Ebracteolati*) Nees in DC., Prodr. 11: 134. 1847.

*Gymnacanthus* Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1854: 126. 1854, not Nees, 1836. TYPE: *Gymnacanthus geminiflorus* (HBK) Oersted (= *R. geminiflora* HBK).

*Copioglossa* Miers, Proc. Roy. Hort. Soc. London 3: 294. 1863. TYPE: *Copioglossa pilosa* Miers.

*Tremacanthus* S. Moore, J. Bot. 42: 33. 1904. TYPE: *Tremacanthus roberti* S. Moore.

*Ulleria* Bremek., Proc. Kon. Ned. Akad. Wetensch. Ser. C. 72, 14: 423. 1969. TYPE: *Ulleria geminiflora* (HBK) Bremek. (= *Ruellia geminiflora* HBK).

Flowers sessile, solitary, borne in the axils of the upper leaves, sometimes in twos by production of supernumerary buds; bracteoles obsolete or absent. Capsule obovoid, thick, with a small solid base ⅓ its length. Seeds (2–)4.

Group *Ebracteolati* is restricted to the New World and consists of several suffruticose herbs common in tropical and subtropical open areas. In South America they exist as a complex of species allied to *R. geminiflora* that is frequent in savannas and campos, in floristic provinces both of the Amazon and Chaco regions or dominions (see Cabrera & Willink, 1980). This group is characterized by a maximum reduction in the structure of the inflorescence (flowers sessile, bracteoles lacking), and by the capsule with a minimum number of seeds.

The subgeneric name *Ebracteolati* was first used by Nees (1847b) under *Dipteracanthus* (Genuini) Nees, but without clear indication of rank. Following article 35 of the *International Code of Botanical Nomenclature* (Greuter et al., 1988), this name is valid provided all other requirements for valid publication are fulfilled, in which case it may act as a homonym or serve as a basionym for future combinations in definite ranks.

**18. Ruellia bulbifera** Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4(3 b): 311. 1895. *Dipteracanthus tuberosus* Nees in C. Martius, Fl. Bras. 9: 42. 1847, not *Ruellia tuberosa* L. 1753. TYPE: Brazil. Without locality: *Sellow s.n.* (holotype, B destroyed; isotype GZU not seen, photo US). Figure 21.

*Ruellia loefgrenii* Lindau, Bull. Herb. Boissier 5: 654. 1897. TYPE: Brazil. São Paulo: in civitate São Paulo ad Feijas in campis, flor. Oct., *Loefgren 997* (holotype, B destroyed, photo F 5933; isotype, C not seen, photo US). Syn. nov.

Sprawling or decumbent herb, with stems to 30 cm long, arising from a woody, rounded or terete, tuberculate xylopodium to 2 cm diam.; stems green, obscurely quadrangular, glabrate, with nodes ± ciliate. Leaves shortly petiolate, widely elliptic, oblong or obovate, 2–4.5 cm long and 1–2 cm wide, rounded at the apex, widely cuneate at the base, the lower ones generally smaller and ± orbicular and retuse, all glabrous and coriaceous, nitidulous on top, with sessile glands and the venation prominent below. Flowers sessile, solitary in the axils of the terminal leaves. Bractlets absent or obsolete. Calyx 1.5–2 cm long, the lobes linear subulate, ca. 1.5 cm long and 2 mm wide, glabrous on the surface, ciliate. Corolla purplish white, 3.5–4.5 cm long, the basal tube ca. 1 cm long, the throat 2–2.5 cm long, the lobes orbicular, ca. 1.5 cm diam. Stamens included, longer ca. 10 mm long, shorter 5 mm long, the anthers 3 mm long. Ovary and style glabrous. Capsule ovoid, 1–1.2 cm long and 7–8 mm thick, broadest at or above the middle, glabrous, the base solid to 3 mm high. Seeds 2–4, brown, ca. 4 mm diam., lightly appressed-puberulous, densely mucilaginous when wet; retinacula 3 mm long.

*Distribution.* Eastern Bolivia, southwestern and southern Brazil, and northeastern Argentina, in dry grasslands, savannas, and campos. It is common on red earth, in recently burnt areas. It flowers in spring and summer, from October to March.

*Representative specimens.* ARGENTINA. **Corrientes:** Depto. Mburucuyá, Estancia Santa Teresa, *Bur-*

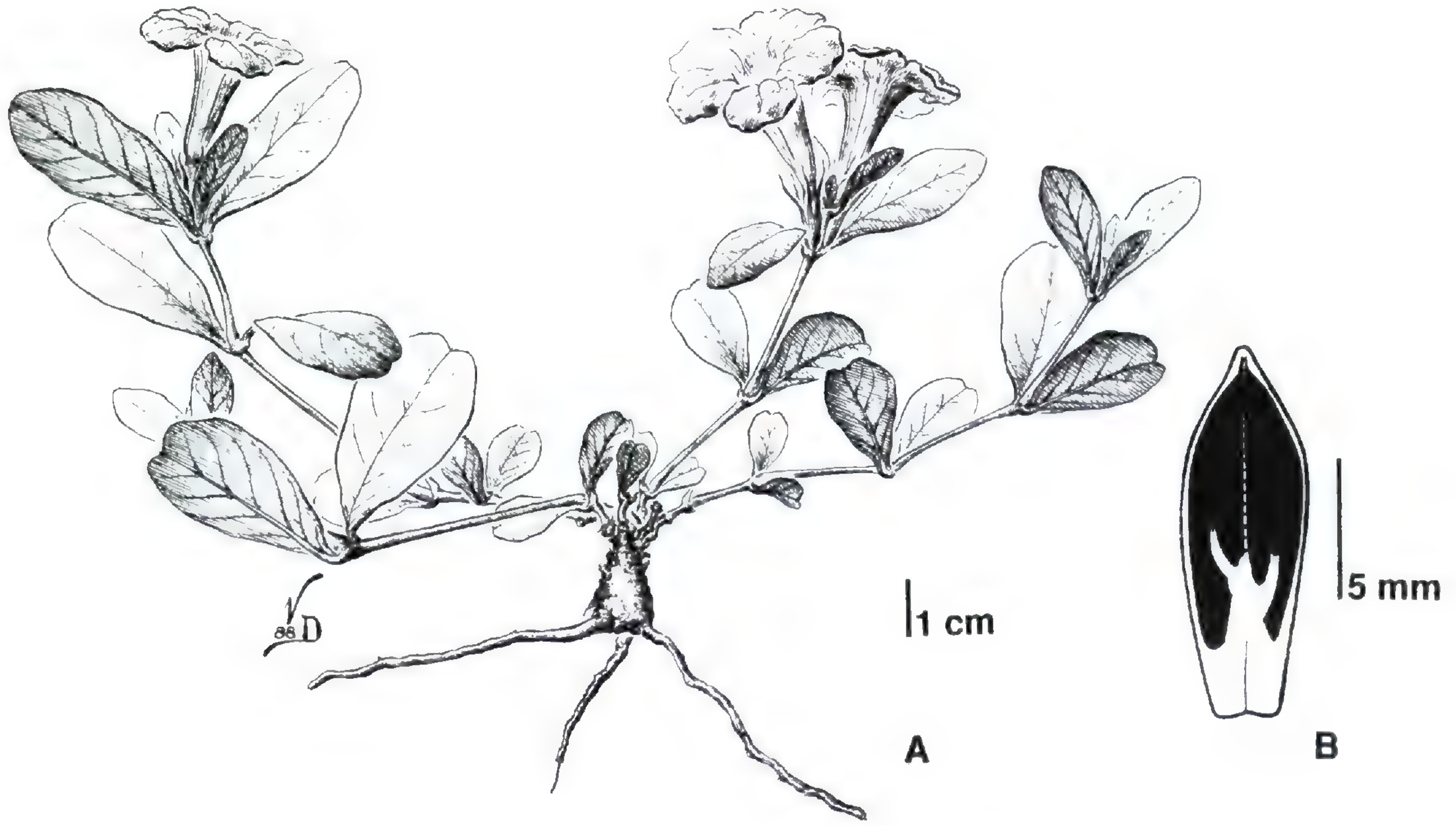


FIGURE 21. *Ruellia bulbifera* Lindau.—A. Habit.—B. Open capsule without seeds, schematic. (A, *Pedersen 5466*; B, *Zuloaga 3133*.)

*kart 19524* (SI); Depto. Santo Tomé, Gobernador Virasoro, *Ibarrola 1220* (LIL); Depto. Ituzaingó, 20 km E de Ituzaingó, *Krapovickas & Cristóbal 16081* (CTES); Depto. Itatí, Ruta 12, 15 km E de acceso a Itatí, *Krapovickas & Cristóbal 20841* (CTES, US); Depto. Santo Tomé, Estancia San Juan Bautista, *Krapovickas 26041* (CTES); Depto. Ituzaingó, Playadito, *Krapovickas 26380* (CTES); Depto. Santo Tomé, Estancia Garruchos, *Pedersen 5466* (LP); Depto. Mercedes, 40 km SW de Carlos Pellegrini, *Schulz 18682* (CTES); 14 km N de Santo Tomé, *Zuloaga 3133* (SI); Ruta 40, entrada a Garruchos, a 2 km del pueblo, *Zuloaga 3138* (SI). **Misiones:** Posadas, *Bertoni 816* (LIL), *Martinez Crovetto 8098, 8163* (BAB); Santa Ana, *Llamas 481* (BAB); Apóstoles, *Martínez Crovetto 8187* (BAB); Depto. San Ignacio, Gobernador Roca, *Martínez Crovetto 8613* (BAB); Concepción de la Sierra, *Martínez Crovetto 8798* (BAB); Loreto, *Montes 3484* (SI), *12414* (LP). BRAZIL. **Paraná:** Ponta Grossa, *Dusén 2724* (R); Turma 23, in campo, *Dusén 16576* (GH); Itararé opposite Morengava, *Dusén 16576* (GH); Mun. Lapa, Engenheiro Bley, *Hatschbach 1000* (LP, MBM, RB); Mun. Arapoti, Rio das Cinzas, Barra do Perdizes, *Hatschbach 7940* (MBM); Mun. Campo Mourão, Campo Mourão, *Hatschbach 12998* (MBM, US). **Rio Grande do Sul:** Cacequi, Macaco Branco, *Eisinger 25* (ICN); Entre Passo Fundo y Carazinho, *Lindeman, Irgang & Valls 8201* (ICN); 20 km SE de Santa Rosa, *Lindeman, Irgang & Valls 8990* pro parte (ICN); Julio de Castilhos, *Palacios & Cuezzo 2558* (LIL); Cruz Alta, *Pivetta 615* (PACA); Canoas, *Rambo 1787* (LIL); Tupanciretam, *Rambo 9596* (PACA); ad montem Sapucaia prope São Leopoldo, *Rambo 38414* (LIL, PACA); Cachoeirinha prope Gravatai, *Rambo 39628* (LIL, PACA). **Santa Catarina:** Abelardo Luz, campo, *Smith & Klein 12852* (HBR, R, US), *13295* (HBR, P, R, US). PARAGUAY. **Boquerón:** Puerto Casado and vicinity, Estancia Palo Santo, *Pedersen 4165* (GH). **Caaguazú:** al S de Yhu, *Fernández Casas 3908B* (G). **Central:** Ipacarí, *Schwarz 10949* (LIL); Patiño, *Teague 574* (BM). **Concepción:** Paraguaria septentrionalis, prope Concepción, *Hassler 7383a* (BM, G, GH, LIL, MO, P); 19 km N de Concepción, camino a Loreto, *Vanni 362* (CTES). **Cordillera:** Cordillère de Piribebuy, *Balansa 4708* (P). **Guairá:** Villa Rica, *Balansa 2464a* (P). **Itapuá:** Encarnación, Colonia Encarnación, *Montes 7125* (SI, US). **Misiones:** 12 km W de San Ignacio camino a Pilar, *Arbo 1884, 1887* (CTES); Santiago, Estancia La Soledad, *Pedersen 4315* (AA, SI); Ruta 4, 20 km E de San Ignacio, *Schinini 21942* (CTES). **Paraguarí:** Paraguari, *Balansa 2464b* (P). **San Pedro:** in regione vicine San Estanislao, *Hassler 4240* (BM, G, K, P); Estancia Carumbé, *Pedersen 8496* (LP); Primavera, *Woolston 888* (PACA, SI, US). **Without locality:** Paraguaria septentrionalis, *Hassler 7383* (BM, G).

*Ruellia bulbifera* is closely related to the widely distributed and variable *Ruellia geminiflora*, from which it could have been derived, but is characterized by the completely glabrous, coriaceous leaves, generally rounded at the apex, and the thick, tuberculate xylopodium. It is easy to identify in its southernmost area, but in Minas Gerais, Brazil, a few specimens with thick, rounded xylopodia do show somewhat pubescent leaves (e.g., *Duarte 4329*, RB).

This species is associated with frequently burnt, open campos and savannas.

**19. Ruellia geminiflora** HBK, Nov. Gen. Sp. 2: 240. 1817. *Dipteracanthus geminiflorus* (HBK) Nees var. *procumbens* Nees in C. Martius, Fl. Bras. 9: 40. 1847. TYPE: Colombia.

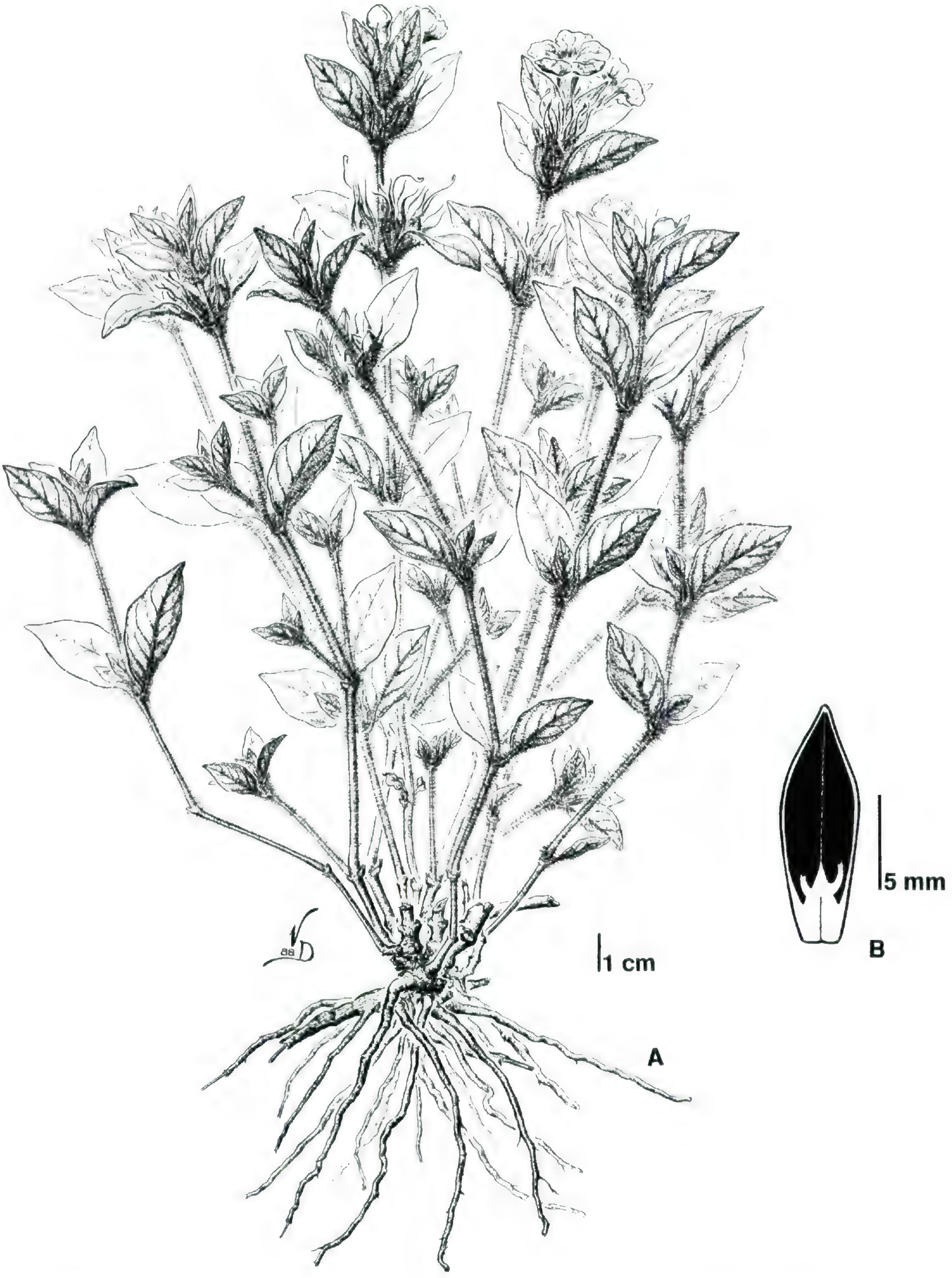


FIGURE 22. *Ruellia geminiflora* HBK.—A. Habit.—B. Open capsule without seeds, schematic. (A, *Cabrera 28119*; B, *Krapovickas 16494*.)

Locis temperatis siccis prope Santa Ana et Ibagué, 500–700 hexapodia, *Humboldt & Bonpland s.n.* (holotype, P, photo F 39431). Figure 22.

*Ruellia hirsuta* Vell. Conc., Fl. Flumin.: 266. 1829. TYPE: Brazil. Illustrated in Fl. Flumin. Icon. 6: t. 96. 1831.

*Dipteracanthus canescens* Nees, London J. Bot. 4: 635. 1844. *Ruellia canescens* (Nees) Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4(3b): 310. 1895. TYPE: Guyana. Without locality, 1837, *Schomburgk 377* (probable isosyntypes, BM, K). Syn. nov.

*Dipteracanthus humilis* Nees in C. Martius, Fl. Bras. 9: 39. 1847. *Dipteracanthus humilis* var. *minor* Nees in C. Martius, Fl. Bras. 9: 39. 1847. SYNTYPES: Brazil. Goias: Natividade, Dec. 1839, *Gardner 3418* (K); Rio Grande do Sul: San Pedro, *Pohl 683* (W not seen, photo F 32746); s. loc., *Sellow s.n.* (B destroyed; isosyntype, K). Syn. nov.

*Dipteracanthus geminiflorus* (HBK) Nees var. *hirsutior* Nees in C. Martius, Fl. Bras. 9: 40. 1847. SYNTYPE: Brazil. Mato Grosso: without collector, *242* (P). Syn. nov.

*Dipteracanthus geminiflorus* (HBK) Nees var. *erectus* Nees, in C. Martius, Fl. Bras. 9: 40. 1847. TYPE: Brazil. Mato Grosso: Padrocinio, *Pohl 673* (syntype, BR; isosyntype, W); without locality: *Sellow s.n.* (syntype, B destroyed; probable isosyntype, K). Syn. nov.

*Dipteracanthus geminiflorus* (HBK) Nees var. *subacaulis* Nees in C. Martius, Fl. Bras. 9: 40. 1847. TYPE: Brazil. Minas Gerais: without locality, *Claussen 678* (probable syntype, K). Syn. nov.

*Dipteracanthus geminiflorus* (HBK) Nees var. *angustifolius* Nees in C. Martius, Fl. Bras. 9: 40. 1847. *Dipteracanthus angustifolius* (Nees) Bremekamp, Rec. d. Trav. Bot. Néerl. 35: 157, t. 14. 1938. TYPE: Venezuela. Carabobo: Valencia, *Moritz s.n.* (holotype, B destroyed). Surinam: without locality or collector (paratype, K herb. Hooker). Trinidad: Savannah, *Lockhart s.n.* (paratype, K herb. Hooker 362). Syn. nov.

*Dipteracanthus porrigens* Nees in C. Martius, Fl. Bras. 9: 41. 1847. SYNTYPES: Brazil. Mato Grosso: Cuyabá, Chapada, *Riedel 63* (isosyntype, GZU not seen, photo US); Piauí: Parnaguá ("Paranagoá"), Aug. 1839, *Gardner 2712* (K; isosyntype, BM); Minas Gerais: without locality, *Sellow s.n.* (syntype, B destroyed; isosyntype, K). Syn. nov.

*Dipteracanthus porrigens* Nees var. *triflorus* Nees in C. Martius, Fl. Bras. 9: 41. 1847. TYPE: Brazil. Ceará: Serra de Araripe, Oct. 1838, *Gardner 1802* (holotype, BM; isotype, US). Syn. nov.

*Dipteracanthus vindex* Nees in C. Martius, Fl. Bras. 9: 42. 1847. SYNTYPES: Brazil. Minas Gerais: in campis ad Contendas, May 1818, *Martius s.n.* (M, photo SI); without locality, *Sellow s.n.* (syntype, B destroyed; isosyntype, K). Syn. nov.

*Copioglossa pilosa* Miers, Proc. Roy. Hort. Soc. London 3: 294. 1863. TYPE: Brazil. São Paulo: Jaraquahiba, *Weir 357* (holotype, BM). Syn. nov.

*Ruellia lindmaniana* Fritsch, Bih. Kongl. Svenska Vetensk. Akad. Handl. 24, Afd. 3(5): 25. 1898. TYPE: Brazil. Minas Gerais: São João d'El Rei, in collibus apricis adustis, qui "campos" vocantur, *Lindmann A 123* (holotype, S).

Suffruticose erect herb, with stems to 50 cm long, from a terete woody rhizome less than 1.5 cm diam.; stems obscurely quadrangular, pubescent, densely white-arachnoid and hirsute at the nodes. Leaves shortly petiolate, widely elliptic, 2–5 cm long and 1–2.5 cm wide, acute at the apex, cuneate at the base, ± white-tomentose, sometimes densely velutinous. Flowers sessile, solitary or geminate in the axils of the terminal leaves. Bractlets absent or obsolete. Calyx 1.5–2 cm long, the lobes linear and subulate, 2 mm wide, densely pubescent. Corolla whitish tinted with purple, 3–4 cm long, the basal tube ca. 1 cm long, the throat 2–2.5 cm long, the lobes orbicular, ca. 1.5 cm diam. Longer stamens ca. 10 mm long, shorter 5 mm long, anthers 2 mm long. Ovary and style puberulous. Capsule obovoid, 1–1.2 cm long and 7–8 mm thick, puberulous, the base solid to 3 mm high. Seeds 2–4, approximately 3 mm diam., appressed puberulous, densely mucilaginous when wetted; retinacula 3 mm long.

*Distribution.* Vastly extended in open grasslands of Central America and the West Indies (Durkee, 1986), and in savannas of South America, from Colombia and Venezuela to eastern Bolivia, southwestern and southern Brazil, Paraguay and northeastern Argentina. A heliophilous species, it is generally found in open sunny places and on sandy ground, in periodically burnt areas. In southern South America it flowers in spring and summer, from October to March.

*Representative specimens.* ARGENTINA. **Chaco:** Ruta 11 y Riacho Iné, *Fabris & Crisci 7148* (LP); Las Palmas, *Jorgensen 2328* (BA, LIL, SI, US); Depto. Bermejo, Arroyo Zapirán, *Krapovickas & Cristóbal 13167* (CTES, US); Río Salado, Ruta 11, *Krapovickas & Cristóbal 13228* (LP, US); Resistencia, *Meyer 476* (SI); Fontana, *Meyer 2833* (LIL); Resistencia, Balneario, *Rojas 12348* (LIL); Depto. 1° de Mayo, Colonia Benítez, *Schulz 108* (BA, LP), *113* (BAB), *784* (CTES), *7417* (LIL), *14114* (CTES). **Corrientes:** Depto. Mburucuyá, Estancia Santa Teresa, *Burkart 19445* (SI, US), *Cabrera 11609* (LP); Depto. San Martín, La Cruz, Tres Cerros, *Cabrera 28119* (SI); Depto. Capital, Arroyo Riachuelo y Ruta 12, *Cristóbal 1148* (CTES); Depto. Itatí, Ramada Paso, *Krapovickas & Cristóbal 16494, 16495* (CTES, SI, LIL, US); Depto. Ituzaingó, Rincón Ombú Chico, *Krapovickas 25603* (CTES); Depto. San Miguel, Loreto, Balneario Municipal, *Mroginski 52* (CTES, SI); Depto. Ita Ibaté, Barranquerita, *Ruiz Huidobro 2077* (LIL); Depto. San Roque, 3 km SE del Rio Santa Lucía, camino a Tobay, Ruta 17, *Schinini & Quarin 7443* (CTES); Depto. Saladas, Pago del Deseo, *Schwarz 145* (LIL);

Depto. General Paz, General Paz, *Schwarz 8475* (LIL); Depto. San Luis del Palmar, Estancia Santa Teresa, *Schwarz 8756* (LIL); Depto. San Cosme, Paso de la Patria, *Tressens 120* (CTES, LIL). **Formosa:** Arroyo Zapirán, *Fabris & Crisci 7079* (LP); Guayculec, *Jorgensen 2847* (BA, LIL, SI); Mojón de Fierro, *Krapovickas 1117* (LIL); Depto. Laishi, Tatané, *Schulz 17079* (CTES). **Misiones:** Santa Ana, *de Llamas 340, 360* (BAB), *Rodriguez 611* (BA, SI); Bonpland, *Jorgensen 137* (BAB, LP, US); Loreto, *Montes 497* (SI); Candelaria, *Montes 835* (LIL); Iguazú, Puerto Istueta, *Montes 10132* (LP); San Ignacio, Santo Pipó, *Schwarz 5356* (LIL); San Pedro, Santa Teresa, *Schwindt 1912* (LIL). **Santa Fe:** Romany, *Martinez Crovetto 4806 1/2* (BAB, LP); Depto. 9 de Julio, Arroyo Golondrina y Ruta 40, *Molina 2011* (BAB). BRAZIL. **Paraná:** Mun. Piraquara, *Hatschbach 2068* (MBM, US); Mun. Jaguariaiava, Façenda das Almas, *Hatschbach 20004* (MBM, US); Mun. Curitiba, Rio Atuba, *Hatschbach 25623, 32729* (MBM, US). **Rio Grande do Sul:** 32 km de Santo Angelo, *Fleig 66* (ICN); Giruá, *Hagelund 4367* (CTES); Granja Piratini, Santo Angelo, *Hagelund 5801, 10391* (CTES); Santo Angelo, *Rambo 53013* (PACA); Pestana, prope Ijuí, *Rambo 57616* (PACA); San Bernardo p. Ijuí, *Rambo 60297* (PACA). **Santa Catarina:** Capinzal, estrada de Capinzal, *Klein 4292* (NBR, US). PARAGUAY. **Amambay:** Parque Nacional Cerro Corá, NE of park headquarters, *Solomon 6819* (MO), *6820* (G, MO); Colonia Yuypyté, 56°W, 23°S, Aeropuerto, *Schinini & Bordas 20507* (CTES). **Caaguazú:** Coronel Oviedo, Ruta 2, km A 140, *Krapovickas & Cristóbal 13424* (CTES, LP). **Canendiyú:** in silva Sierra de Maracayú, *Hassler 5382* (G). **Central:** Margen S del Río Salado, camino de Limpio a Emboscada, *Arbo 1671* (CTES); L'Assomption, *Balansa 2463a* (P); Ita Ibaté, *Degen 321* (G); Prope lacus Ypacarai, *Hassler 3219* (BM, G); Areguá, *Mereles 1639* (G); Patiño, *Teague 577* (BM). **Concepción:** zwischen Río Apa und Río Aquidaban, Centurion, *Friebrig 5239* (G); prope Concepción in rupestribus, *Hassler 7257* (G). **Cordillera:** San Bernardino, *Hassler 1538, 3360* (G); San Bernardino, costa del lago Ypacaray, *Quarín 1540* pro parte (CTES, US); Valenzuela, Río Y-hacá, *Sparre & Vervoorst 1159* (LIL). **Guairá:** Villa Rica, *Jorgensen 4123* (GH, LIL, MO, NY, SI, US), *4126* (NY, US); Doña Juana, près de Villa Rica, dans les prairies, *Balansa 2463* (G, P); Cordillera de Ybytyruzú, road to Cantera Jhú, *Zardini 15275* (MO). **Misiones:** 12 km W de San Ignacio, camino a Pilar, *Arbo 1886* (CTES, US). **Neembucú:** Curupaity, *Schulz 7969* (CTES). **San Pedro:** in regione vicinis San Estanislao, *Hassler 4238* (P); Primavera, *Woolston 775* (LIL, NY, SI, US). **Without locality:** in silva prope Arroyo Mocoy, *Hassler 4904* (G); central Paraguay, *Morong 659* (BM, NY, US), *854* (GH).

*Ruellia geminiflora* is characterized by the somewhat thick, fibrous roots, the pubescent stems, the more or less ovate, pubescent leaves, the axillary sessile flowers that lack bracteoles, and the thick, obovoid, few-seeded capsule. It is an extremely variable species with a wide distribution that presents many local forms. These have frequently been given varietal or specific status and names.

Nees recognized five varieties for Brazil (1847a, b): *procumbens, hirsutior, erectus, subacaulis,* and *angustifolius*. Several other species that have been described for South America are also obviously related to *Ruellia geminiflora*. It is sometimes difficult to decide if they should be treated as separate taxonomic entities of a wide *Ruellia geminiflora* complex, or to include them within a single species as ecotypes, without giving them formal taxonomic recognition. Here *Ruellia geminiflora* is presented in its wider sense, and the names of several local variants have been reduced to synonymy. Such is the case of populations with narrow leaves that have been described as *Dipteracanthus canescens* Nees, *Dipteracanthus geminiflorus* var. *angustifolius* Nees, *Dipteracanthus humilis* Nees, or *Dipteracanthus vindex* Nees. These small, narrow-leaved forms appear in different areas of South America (central and southern Brazil: Minas Gerais, Mato Grosso do Sul, and Rio Grande do Sul; Guyana; Venezuela) and may be the result of parallel evolution within the species, or of long-distance dispersal phenomena, probably associated with migrating birds that could carry the mucilaginous seeds from one region to another. Such is also the case of the larger, more robust and branched shrubby plants with variable coriaceous leaves that are frequent in northeastern, central, and southwestern Brazil, and have been described as *Ruellia porrigens* Nees. Some specimens of eastern Paraguay, such as *Hassler 5382* from Canendiyú, or *Schinini 20507* and *Solomon 6819* and *6820* from Amambay, fall into this category. This form could be the result of edaphic conditions or of continuous growth related to an accidental absence of periodic fires during several successive growing seasons in some areas. A similar case is that of short-stemmed, nearly acaulescent populations described as variety *subacaulis* or *Ruellia lindmaniana*, which may be the response of the plants to the shortening of the growing period by the action of burning. Although some of these forms may deserve subspecific status, to decide on this a thorough study of the morphological and ecological diversification of the species throughout Central and South America should be undertaken.

Specimens of *Ruellia geminiflora* from Paraguay have been mistakenly identified by Morong & Britton (1892–1893) as *Ruellia bahiensis* (Nees) Morong. *Ruellia bahiensis* is another species of group *Ebracteolati*, which is very similar, but inhabits a different area and differs by the markedly swollen nodes of the stems and the somewhat accrescent calyces that remain attached to the leaf axils after the shedding of the capsules. It is found in northeastern Brazil.

**20. Ruellia magniflora** Ezcurra, sp. nov. TYPE: Paraguay. Central: Villa Elisa, sandy fields, *Pedersen 6522* (holotype, LP). Figure 23.

Herbae perennes ad basim suffruticosae, radicibus fasciculatis fibrosis crassis, ramis ascendentibus 30 cm altis parce ramificatis velutino-pubescentibus. Folia subsessilia anguste oblonga vel lanceolata, 5–9 cm longa 1.5–2 cm lata, apice acuta basi cuneata, argentea, utrimque velutino-tomentosa. Flores sessiles, solitarii vel geminati, in axillis foliorum terminalium dispositae, bracteolis obsoletis. Calycis segmenta linearia ca. 2 cm longa 1.5 mm lata extus pubescentia dense ciliata. Flores caerulei 5–7 cm longi. Corollae infundibuliformis tubo faucibus breviore, lobis rotundatis. Antherae inclusae. Stylus filiformis. Capsula obovata, 1 cm longa 0.8 cm crassa, puberula, 4-sperma. Semina 3 mm longa, in siccus adpresso puberula.

Suffruticose herbs from a small, woody rhizome, with thick, fleshy, fusiform roots. Stems erect, to 30 cm long, velutine-puberulous. Leaves shortly petiolate, narrowly oblong or lanceolate, 5–9 cm long and 1.5–2 cm wide, acute and cuneate, grayish velutine-tomentose, the lowermost somewhat shorter and obtuse. Flowers sessile, solitary or in twos in the axils of the terminal leaves. Bractlets obsolete. Calyx 2 cm long, the lobes linear, ca. 1.5 mm wide, pubescent, densely ciliate. Corolla pale blue, 5–7 cm long, the basal tube 1.5–2 cm long, the throat 2.5–3.5 cm long, the lobes orbicular, ca. 2.5 cm diam. Longer stamens ca. 1 cm long, shorter stamens 0.5 cm long, anthers 3 mm long. Ovary and style glabrous. Capsule obovoid, 1 cm long and 0.8 cm thick, puberulous, 2–4-seeded, the base solid to 2.5 mm high. Seeds 3 mm diam., appressed-puberulous, densely mucilaginous when wet; retinacula 3 mm long.

*Distribution.* Common on sandy savannas of eastern Paraguay, southwestern Brazil, and northeastern Argentina. It flowers in spring and summer.

*Representative specimens.* ARGENTINA. **Corrientes:** Depto. Mburucuyá, Estancia Santa Teresa, *Pedersen 9844* (CTES); Villa Olivari, 18 km W de Ituzaingó, *Schinini 15664* (CTES); Ituzaingó, Estancia Santa Tecla, *Schwarz 8039* (LIL); Ruta 12, 20 km E de Ituzaingó, *Zuloaga 3220* (SI). BRAZIL. **Mato Grosso do Sul:** Gouveia, Fazenda, campo rupestre, *Cerati 33790* (SPF); Mun. Rio Brilhante, Rio Vacaria, *Hatschbach 25186* (MBM). PARAGUAY. **Amambay:** Parque Nacional Cerro Corá, ca. Cerro Guaiguy Hog, *Fernández Casas 4016* (G); 7 km N de la Ruta 5 limite W del Parque Nacional Cerro Corá, *Ferrucci 701* (CTES). **Concepción:** zwischen Río Apa und Río Aquidabán, Villa Sana, *Fiebrig 4843, 4882* (G). **Cordillera:** in pratis prope San Bernardino, *Hassler 110* (G); in silva Caraguatay, *Hassler 3333* (G); in dumeto prope Caraguatay, *Hassler 4592* (G); Barranca Arroyo Y-haca, *Teague 108* (BM); iter ad yerbales montium "Sierra de Maracayú," *Hassler 4238* (BM, G).

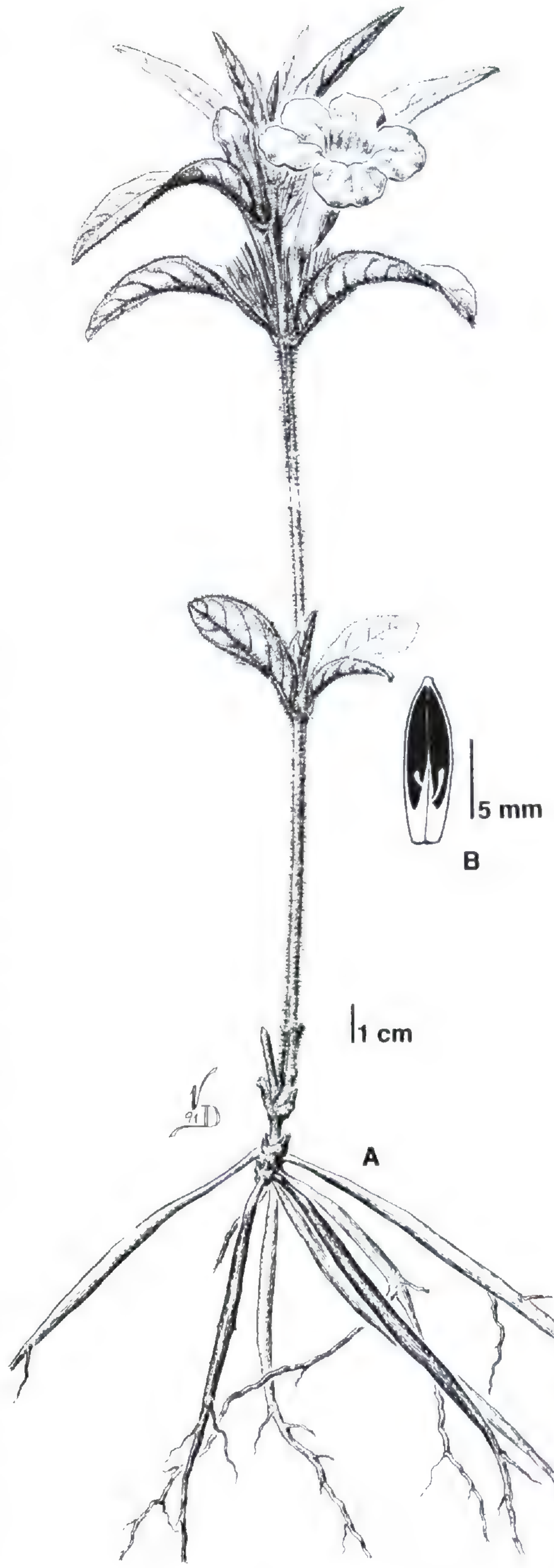


FIGURE 23. *Ruellia magniflora* Ezcurra.—A. Habit.—B. Open capsule without seeds, schematic. (A, *Pedersen 6522*; B, *Hassler 110.*)

*Ruellia magniflora* is clearly allied to *Ruellia geminiflora*; it differs by its fleshy, fusiform, tuberous roots, its narrow, lanceolate, longer leaves, and by its larger, pale-blue flowers.

## VI. Group **Salpingacanthus**

*Salpingacanthus* S. Moore, J. Bot. 42: 107. 1904. TYPE: *S. nobilis* S. Moore.

Flowers sessile, in the axils of the upper leaves; bracteoles obsolete. Calyx segments unequally cleft, forming a three-lobed structure. Capsule oblong in shape, with a small solid base ¼ its length. Seeds ca. 8.

The only species of this group is remarkable because of its large, white, sphingophilous flowers, with a long basal tube and exserted stamens. It is found in a small area of southwestern Brazil and northern Paraguay, in eastern Chaco forest.

Group *Salpingacanthus* shows no close affinities with any other groups in the area.

**21. Ruellia nobilis** (S. Moore) Lindau, Feddes Repert. 7: 67. 1909. *Salpingacanthus nobilis* S. Moore, J. Bot. 42: 107. 1904. SYNTYPES: Brazil. Mato Grosso do Sul: Corumbá, *Robert 713a*, *Robert 800* (BM; isosyntypes, NY). Figure 24.

Suffruticose herb or straggling shrub with the stems sparsely branched, terete, glabrous, pale at maturity. Leaves on petioles 0.5–1.5 cm long, the blades widely ovate, 4–10 cm long and 2.5–5 cm wide, acuminate, rounded on the base and somewhat decurrent on the petiole, the margin entire, the surface lightly velutine-puberulous, especially on the underside, the secondary veins parallel and prominent beneath. Flowers subsessile, solitary in the axils of the upper leaves. Bracteoles obsolete. Calyx 2–3 cm long, unequally cleft, lower segments united with the lateral ones, the posterior free, forming a three-lobed structure, the lobes 2 cm long and 1 cm wide, puberulous, light green in color. Corolla white, ca. 10 cm long, the basal tube 7–9 cm long, the throat obconic, 1–2 cm long and 1 cm diam., the lobes white, spreading, suborbicular, 2.5 cm wide. Stamens subexserted, filaments ca. 1.5 cm long, anthers 5 mm long. Ovary and style glabrous. Capsule oblong-elliptic in shape, 1.5–3 cm long and 4–5 mm thick, with a solid base to 0.5 cm, the surface glabrous. Retinacula 4 mm long; seeds 6–8, 3–4 mm diam., glabrous, pubescent and mucilaginous when wet.

*Distribution.* Southwestern Brazil and northern Paraguay, in eastern Chaco forest. *Ruellia nobilis* flowers in spring.

*Representative specimens.* BRAZIL. **Mato Grosso do Sul:** Corumbá, in dumetis silvulisque daris regionis calcaridis, *Malme 2747* (S); Corumbá a 200 m da divisa, Bolivia, cerrado estrada do Jacadigo, *Almeida 1713* (RB). PARAGUAY. **Alto Paraguay:** Fuerte Olimpo, Chaco Paraguayo, *Rojas 13638* (CTES, G, LIL, US).

*Ruellia nobilis* in the Acanthaceae and *Sphingiphila tetramera* (Gentry, 1990) in the Bignoniaceae appear to show convergent evolution with respect to corolla morphology. Both species, endemic to the same area (northeastern Paraguayan Chaco, and limiting areas of Brazil and Bolivia in the case of *Ruellia nobilis*), present a presumably sphingid-adapted corolla tube of the same size and proportions, attaining a length of more than 10 cm, a remarkable feature in both families. This probably reflects the selective pressure of the same type of pollinator acting in this area.

## VII. Group **Chiloblechum**

*Blechum* Nees subg. *Chiloblechum* Oersted, Vidensk. Meddel. Dansk Naturhist. Foren. Kjobenhavn 1854: 169. 1854. TYPE: *Blechum mexicanum* Oersted (lectotype, here selected).

*Penstemonacanthus* Nees in C. Martius, Fl. Bras. 9: 159. 1847. TYPE: *Penstemonacanthus modestus* Nees. Syn. nov.

Flowers sessile and solitary, ebracteolate, subtended by the upper leaves sometimes transformed into bracts, forming terminal spikes. Calyx frequently zygomorphic, the lateral lobes united with the two anterior, the posterior one free. Capsules ovate in shape, with a small solid base; placentas that separate elastically from the capsule with the retinacula and the seeds, breaking the walls. Seeds 4–8.

The species of this group occur in southern North America and subtropical South America, in a disjunct distribution. The two South American species are herbs with a suffruticose base and produce brilliant blue flowers that appear psychophilous.

Group *Chiloblechum* differs markedly from the rest of the genus in the structure of the fruit, in which the placentas, with the retinacula and the seeds, separate elastically from the walls of the capsule. This character also appears in other genera of Acanthaceae (e.g., *Blechum*, *Tetramerium*, *Dicliptera*, some *Justicia*) that do not seem to have close evolutionary relationships with *Ruellia*, and therefore could be a case of parallel evolution within the family. However, the genus *Blechum* is morphologically closely related to *Ruellia* (Bremekamp & Nannega Bremekamp, 1948), and has the same structure of the capsule correlated with the same inflorescence morphology as species of

FIGURE 24. *Ruellia nobilis* (S. Moore) Lindau. — A. Flowering branch. — B. Open capsule without seeds, schematic. (A, B, *Rojas 13638.*)

*Ruellia* sect. *Chiloblechum*, differing only in the size of the flowers and the pollen morphology. In this case, reticulate evolution could also explain the morphology of the species of group *Chiloblechum*, which have characters in common both with *Ruellia* and *Blechum*.

**22. Ruellia erythropus** (Nees) Lindau in Engl. & Prantl, Nat. Pflanzenfam. 4, Abt. 3b: 311. 1895. *Siphonacanthus erythropus* Nees in C. Martius, Fl. Bras. 9: 47. 1847. TYPE: Brazil. Rio Grande do Sul: Porto Allegre, São Lourenço, *Sellow s.n.* (holotype, B destroyed, photo F 5920; isotype, K). Figure 25.

*Penstemonacanthus modestus* Nees in C. Martius, Fl. Bras. 9: 159. 1847. TYPE: Brazil. Minas Gerais: Caatingas ad Contendas, July, *Martius s.n.* (holotype, M not seen, photo F 20573). Syn. nov.

*Blechum tweedii* Nees in DC., Prodr. 11: 466. 1847. *Ruellia tweedii* (Nees) T. Anderson ex Morong & Britton, Ann. New York Acad. Sci. 7: 192. 1893. TYPE: Argentina. Paraná? ("Panama"): without locality, *Tweedie s.n.* (holotype, K). Syn. nov.

*Blechum mexicanum* Oersted, Vidensk. Medd. Naturhist. For. Kjobenhavn 8–12: 169, tab. 5, f. 1–4, 1854. TYPE: Mexico. Vera Cruz: "Antigua og paso de Doña Juana, Hacienda de Santa Barbara, Morro de Boquilla, Rancho Nuevo," *Liebmann s.n.* (holotype, C not seen).

*Ruellia pubiflora* Griseb., Abh. Königl. Ges. Wiss. Göttingen 24: 259. 1879. TYPE: Argentina. Salta: San José, Orán, Laguna del Palmar, *Lorentz & Hieronymus 550* (holotype, GOET not seen, photo SI; isotype, NY).

*Ruellia matogrossensis* Lindau, Bull. Herb. Boissier 3: 362. 1895. TYPE: Brazil. Mato Grosso: Jacobina, *Kuntze s.n.* (holotype, B destroyed, photo F 5936; isotype, NY). Syn. nov.

*Ruellia velascana* Lindau, Bull. Herb. Boissier 3: 363. 1895. TYPE: Bolivia. Santa Cruz: prov. Velasco orientali, 200 m, *Kuntze s.n.* (holotype, B destroyed, photo F 18222; isotype, NY). Syn. nov.

Erect or straggling suffruticose perennial 20–60 cm tall, with a ligneous base and tough, fibrous roots. Stems thin, decumbent, obtusely quadrangular, somewhat woody and rooting at the lower nodes, generally glabrous. Leaves on slender petioles 0.3–1 cm long, the blade elliptic or ovate, 2–6 cm long and 1–2.5 cm wide, acute or acuminate, cuneate on the base, generally glabrous on the surface and with sessile patelliform glands beneath, the margin entire. Flowers sessile, solitary in the axils of the upper leaves, in terminal, densely foliose spikes. Bracts (upper leaves) opposite and decussate, imbricate, similar to the normal leaves but subsessile, smaller and ciliate. Bractlets obsolete. Calyx ca. 5 mm long, unequally cleft, the two lateral segments united to the two lower ones, the posterior free, forming a three-lobed structure. Corollas erect, blue, 2.5–3.5 cm long, the basal tube 1.5 cm long, the throat campanulate-obconic, 1–1.5 cm long, the lobes spreading, orbicular, ca. 8 mm long. Stamens included, long filaments ca. 8 mm, short 5 mm, the anthers 3 mm long. Ovary and style glabrous. Capsule ovate, 1 cm long and 4 mm thick, the lower 3 mm solid, puberulous, glabrescent. Placentas breaking away with the retinacula and the seeds from the dry mature capsule. Retinacula 2–3 mm long; seeds 4–8, dark, 2–3 mm diam., with mucilaginous hairs when wet.

*Distribution.* Mexico (Yucatan and Veracruz), southeastern Bolivia, Paraguay, southern, southeastern, and southwestern Brazil, and northern Argentina. In South America it is frequent in the understory of Chaco forest and adjacent brevideciduous transition forests. It flowers in winter and spring, from June to October.

*Representative specimens.* ARGENTINA. **Catamarca:** entre Los Altos y La Viña, *Morello 1160* (LIL); Depto. Paclín, Cuesta del Totoral, *Rodrigo 3184* (LP); Depto. El Alto, Balengua, *Venturi 7069* (SI, US). **Chaco:** Colonia Benítez, *Cabrera 2982* (LP), *Schulz 12290* (CTES, US); Las Palmas, *Jorgensen 2327* (LIL, SI, US); Ruta 11, Arroyo Canguí Chico, *Krapovickas 13175* (LP, US); Resistencia, *Krapovickas 15846* (CTES, SI, US); Enrique Urien, *Rodrigo 2702* (LP); Roque Sáenz Peña, *Schulz 2497* (CTES); Depto. Güemes, La Fidelidad, Río Teuco, *Schulz 15594* (CTES), *16348* (US). **Corrientes:** Paso de la Patria, *Cabrera 18555* (CTES); Depto. Empedrado, El Pollo, *Ibarrola 3189* (LIL); Garruchos, San Juan Bautista, *Krapovickas 25767* (CTES); Arroyo Chirimay, *Krapovickas 26164* (CTES, US); Perichón, *Krapivockas 26451* (CTES, US); Balneario Molina Punta, *Schinini 11578* (CTES, US); Corrientes, costa del Río Paraná, *Tressens 784* (CTES). **Entre Ríos:** Paraná, La Toma, barrancas, *Burkart 23827* (SI); Paraná, Toma Nueva, *Correa 19015* (SI); Paraná, barrancas, *Fabris 47* (LIL); Paraná, barrancas orillas Paraná, *Meyer 10146* (LIL). **Formosa:** Ruta 83, 8 km N de Ing. Juárez, *Correa 7670* (BAB); Ruta 11 y Río Bermejo, *Fabris 7194* (CTES); Ruta 81, 32 km al N de Las Lomitas, *Fortunato 475* (BAB); 10 km S de Riacho Negro, *Krapovickas 13070* (CTES, LP, US); Pirané, *Morel 1258* (LIL); 2 km al N de Porteñito, *Morel 2985* (LIL, US); Pilagá, *Pierotti 4213* (LIL, US); Mojón de Fierro, *Schulz 157* (BAB); Entre Palo Santo y Los Matacos, *Schulz 18300* (CTES). **Jujuy:** Vinalito, *Cabrera 4113* (LP); El Piquete, *Cabrera 14565* (LP); Cerros al SE de San Pedro, *Cabrera 16057* (LP); Rio Zapla, *Cabrera 20804* (LP); Camino a Valle Grande, Tres Cruces, *Cabrera 27890* (SI); Entre Mesada de las Colmenas y Aguas Negras, *Cabrera 32157* (SI); Chalicán, *Cabrera 34102* (SI); Palma Sola, *Fabris 3133* (LP); Calilegua, *Fabris 4425* (LP); Cuesta Las Lajitas, *Kiesling 99* (LP); Santa Clara, *Venturi 9658* (LP, MO). **Misiones:** San Ignacio, *Birabén 5284* (LP); Apóstoles, Escuela Agrotécnica, *Cabrera 28503* (SI); Candelaria, Santa Ana, *Montes 1572* (LIL, US); Salto Iguazú, Puerto Aguirre, *Rodriguez 353* (BA); Puerto Aguirre, *Rojas*

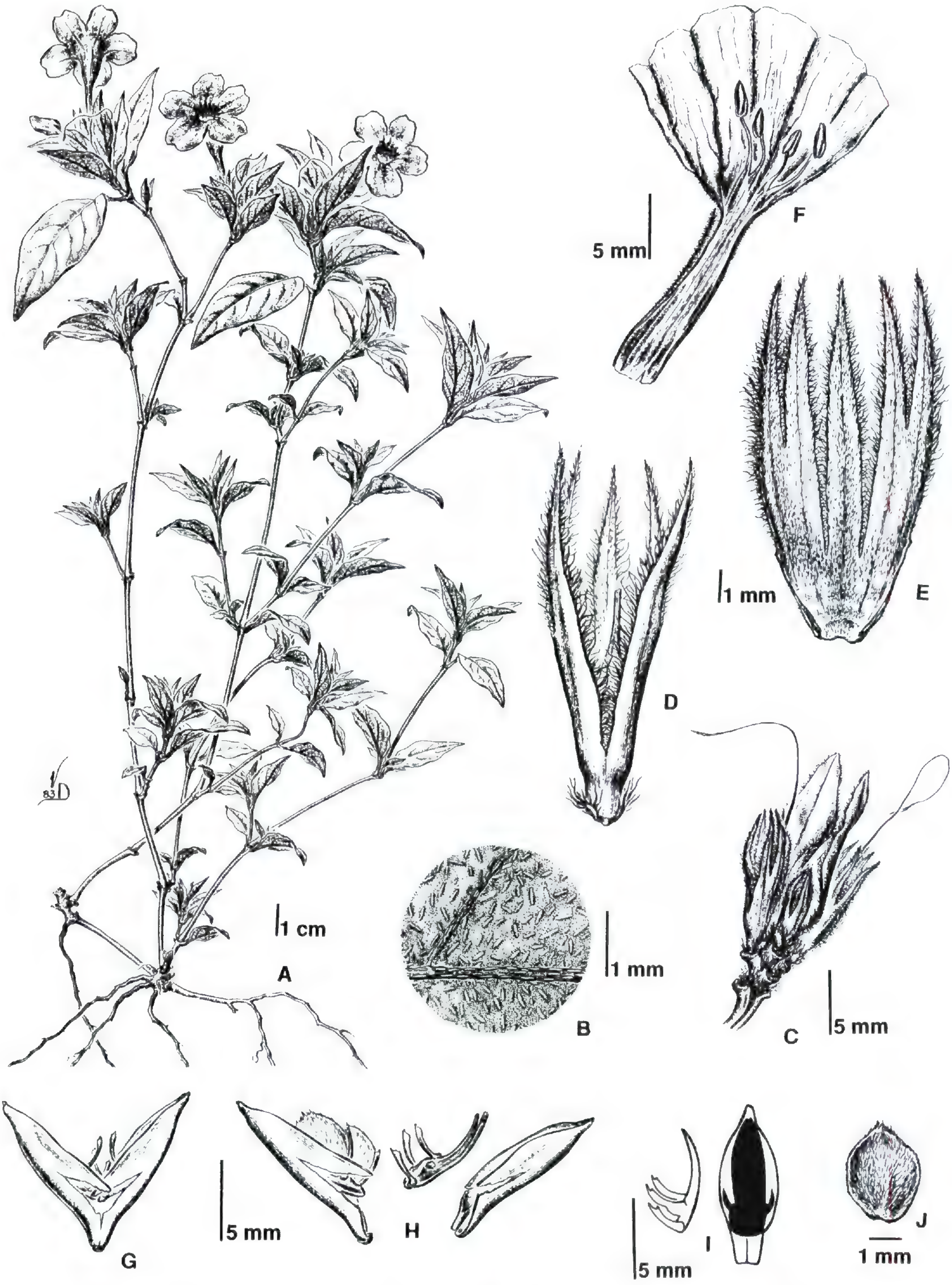


FIGURE 25. *Ruellia erythropus.*—A. Habit.—B. Abaxial leaf surface with cystoliths.—C. Inflorescence apex, showing calyces.—D. Calyx.—E. Open calyx.—F. Open corolla, showing stamens.—G. Dehiscent capsule with broken walls, without seeds, schematic.—H. Capsule valves with placenta, retinacula and seeds separating.—I. Open capsule without seeds, the placenta separated.—J. Seed. (A–H, J, *Cabrera 32157*; I, *Cabrera 28503.*)

*8073* (LIL); Bernardo de Irigoyen, *Schwindt 4201* (LIL). **Salta:** Orán, *Cabrera 4575* (LP); Tartagal, ruta a Pozo de la Cuchara, *Correa 7726* (BAB); Rivadavia, 15 km al S de Palmarcito, *Cuezzo 695* (LIL); Parque Nacional El Rey, *Ezcurra 371* (SI); General Ballivián, *Maldonado 764* (LP); La Caldera, *Rosa 183* (SI); Joaquín V. González, *Rossi 1064* (LP); Taratagal, Zanja Honda, *Schreiter 3429* (LIL); Depto. Anta, La Salada, *West 412* (LIL). **Santa Fe:** Villa Guillermina, *Meyer 2999* (LIL); 2 km E de Villa Guillermina, *Pensiero 1580* (SI); Mocoví, *Venturi 18* (LIL, LP, SI, US). **Tucumán:** Horco Molle, *Fabris 6531* (LP); Tafí, Villa Nougues, *Lillo 12023* (LIL); Trancas, *Maldonado 401* (LP); Burruyacu, La Ramada, *Rocha 496* (LIL, US); Quebrada de Lules, *Venturi 2292* (BAB, LIL, LP, SI, US); Santa Rosa, *Venturi 353* (LIL, SI, US); Tafí Viejo, *Venturi 2295* (LIL); Yerba Buena, *Vervoorst 8623* (LIL). BRAZIL. **Paraná:** Mun. Foz do Iguaçú, Paraná, Ocoi, *Buttura 559* (MBM); Mun. Candido Rondon, Corrego R. Branco, *Hatschbach 43996* (MBM, US); Mun. Roncador, Cancan, *Hatschbach 32901* (MBM, US). **Rio Grande do Sul:** Rio Jacuhy, *Bornmüller 637* (GH); Balneario Ivaí, *Arzivenco s.n.* (ICN); Parque do Balneario Ivaí, *Torgo 53* (US). MEXICO. **Veracruz:** Paso del Macho, Rancho Paso Grande, *Calzada 3010* (IPN); Mun. Dos Ríos, Miradores, *Ventura A. 9542* (IPN); Mun. Naolinco, La Meza, *Ventura A. 15791* (IPN). **Yucatán:** Chichén Itzá, *Paray 1522* (IPN); Mérida, Cruz de Gaher, *Seler 3948* (K, US); Yucatán, *Valdez 24* (K). PARAGUAY. **Boquerón:** Col. Fernheim, 30 km W de Filadelfia, *August 111* (CTES). **Canendiyú:** in campo Ipé Hu, *Hassler 5309* (G); in regione yerbalium de Maracayú, *Hassler 4203* (AA, BM, G, NY, P, MO). **Central:** La Trinidad, *Balansa 2458* (G, P); in regione lacus Ypacaray, *Hassler 12200* (BM, G, GH, LP, MO, NY, US); Villa Elisa, *Pedersen 6521* (AA, LP). **Chaco:** Parque Nacional Defensores del Chaco, *Fernandez Casas 4365* (G); Río Verde, *Herter 5024* (GH, MO, US); Mayor Pedro Lagerenza, *Schinini & Bordas 15045* (CTES, US). **Concepción:** San Salvador, *Balansa 2458a* (P); zwischen Río Apa und Río Aquidaban, Puerto Risso, *Fiebrig 4048* (BM, G); prope Concepción, *Hassler 7178* (AA, BM, G, P). **Cordillera:** San Bernardino, *Hassler 312* (G, SI); in silva Caraguatay, *Hassler 3121* (AA, BM, G, NY, P). **Guairá:** Común en el Monte Haití, *Jorgensen 4306* (GH, LIL, LP, MO, NY, RB, SI, US). **Paraguarí:** Paraguarí, *Balansa 2458b* (P); Macizo Acahay, *Zardini 6633, 6927* (MO, US). **Presidente Hayes:** in regione cursus inferioris fluminis Pilcomayo, *Rojas 156* (BM, G); Pilcomayo River, *Morong 967* (BM, G, GH, US); Estancia Pozo Favorito, *Spichiger 1506* (G). **San Pedro:** Colonia Primavera, *Woolston 570* (GH, LIL, SI, US).

*Ruellia erythropus* is characterized by the blue flowers in terminal spikes, with the leaves subtending the flowers subsessile and ciliate, somewhat morphologically different from those on the lower vegetative portion of the shoot, and therefore appearing like bracts. Also, the placentas separate elastically from the capsule with the retinacula and the seeds. In these characters it approaches the closely related genus *Blechum*, which differs in pollen morphology.

*Ruellia erythropus* has an extremely extended range in subtropical South America, and a curious disjunct distribution, having been described also for Veracruz and Yucatán, Mexico, as *Blechum mexicanum*. Although I have not seen the type specimen of *B. mexicanum*, I have studied material from Mexico to verify this synonymy (see list of representative specimens). The name *Ruellia erythropus* precedes the name *R. tweedii*, with which this species had been cited by most previous authors (e.g., Ariza Espinar, 1983; Dawson, 1979; Leonard, 1936; Morong & Britton, 1892–1893). The extensive synonymy of this species reflects the wide range it inhabits and its associated morphological variation. It is somewhat similar to *Ruellia bahiensis* from northeastern Brazil (of group *Ebracteolati*), but differs by the inflorescence and capsule structure. Several herbarium specimens of *Ruellia erythropus* from Paraguay and Argentina have been erroneously identified as *Ruellia bahiensis*.

Although the genus *Penstemonacanthus* was described by Nees (1847a) based on material supposedly having five stamens, it is an exception, not only in this species but in all the genus *Ruellia*, and probably a teratology. The rest of the morphological characters of the original description of *Penstemonacanthus modestus* clearly agree with those of *Ruellia erythropus*. Although I have not investigated the structure of the capsule in the photograph of the type, it has been clearly described by Nees in both the genus and species descriptions.

**23. Ruellia hypericoides** (Nees) Lindau in Engl., Bot. Jahrb. 19, Beibl. 48: 16. 1894. *Dipteracanthus hypericoides* Nees in C. Martius, Fl. Bras. 9: 39. 1847. SYNTYPES: Brazil. Rio Grande do Sul: without locality, *Sellow s.n.* (B destroyed, photo F 5931; isosyntype, K); without locality, *Gaudichaud 244* (P). Figure 26.

Delicate herb 15–25 cm tall, from a small basal rhizome with fibrous roots. Stems weak, erect or decumbent, terete, shortly appressed-pubescent, with long internodes. Leaves shortly petiolate, ovate or orbicular, 1.5–2 cm long and 0.8–1.3 cm wide, obtuse or rounded in the apex, truncate in the base, the lower ones smaller, all puberulous on top and densely dotted with sessile patelliform glands on the surface beneath, the margins entire. Flowers sessile, solitary in the axils of the upper leaves. Bracteoles obsolete. Calyx 5 mm long, the segments linear-lanceolate, 4 mm long and 1 mm wide, acute, appressed-puberulous and ciliate. Corolla erect, blue, 2–3 cm long, the basal tube 1.2–1.5 cm long, the throat campanulate-obconic, 5–6 mm long and 4–5 mm diam., the lobes spreading, suborbicular, ca.

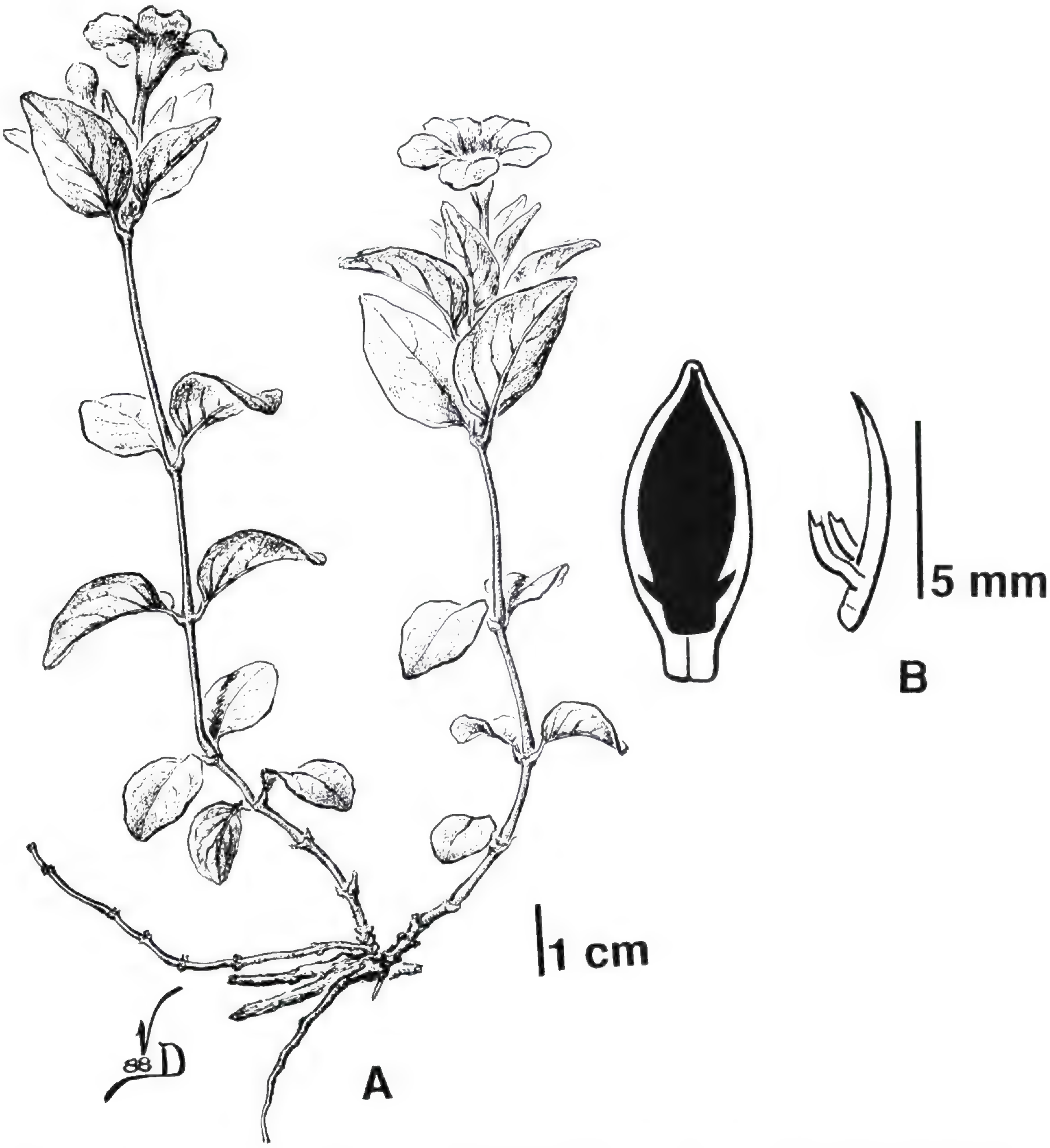


FIGURE 26. *Ruellia hypericoides* (Nees) Lindau.—A. Habit.—B. Open capsule without seeds, schematic, the placenta and the retinacula separated. (A, B, *Burkart 14181.*)

8 mm diam., somewhat emarginate. Stamens included, ca. 7 mm long, anthers 2 mm long. Ovary and style puberulous. Capsule ovate, 7–9 mm long and 4 mm thick, puberulous, the base solid. Placentas breaking away with the retinacula and the seeds from the dry mature capsule. Retinacula 1.5 mm long; seeds 4–8, brown, 2 mm diam., with mucilaginous hairs when wet.

*Distribution.* Southern Brazil, southern Paraguay, northeastern Argentina, and northern Uruguay. *Ruellia hypericoides* is found in open, grassy campos. It flowers in spring and summer, from November to February.

*Representative specimens.* ARGENTINA. **Corrientes:** Ituzaingó, Estancia San Miguelito, 20 km NE de Playadito, Ruta 39, *Carnevali 5044* (CTES); Ituzaingó, Estancia Santa Rita, *Correa 8219* (BAB); Santo Tomé, Estancia Garruchos, Cachuera, Arroyo Chirimay, *Krapovickas 21215* (US), *21216* (CTES); Santo Tomé, R.40 y Arroyo Chirimay, *Krapovickas 10682* (CTES); Santo Tomé, Estancia Garruchos, *Krapovickas 21407* (CTES);

Ituzaingó, Ruta 39, 30 km N de Virasoro, *Krapovickas 25341* (CTES); Ituzaingó, San Carlos, *Martínez Crovetto 8020* (BAB); Ituzaingó, Estancia Puerto Valle, *Partridge s.n.* (LP); Santo Tomé, Estancia Garruchos, *Pedersen 985* (AA), *5434* (AA, ICN, LP). **Misiones:** Apóstoles, Pindapoy, *Birabén 5396* (LP); Posadas, *Burkart 14181* (SI), *Martínez Crovetto 8153, 8164* (BAB); Concepción, Mártires, *Martínez Crovetto 6207* (BAB); San Ignacio, Gob. Roca, *Martínez Crovetto 8621* (BAB); Posadas, *Meyer 6010* (LIL); Frontera, San Antonio, *Montes 7074* (SI, US); San Ignacio, Santo Pipó, *Schulz 7213* (LIL); Posadas, *Spegazzini 19397* (SI); Depto. Apóstoles, Arroyo Chirimay, balneario Azara, *Tur 1927* (SI); de Apóstoles a Concepción de la Sierra, Arroyo Las Tunas, *Zuloaga 3248* (SI). BRAZIL. **Rio Grande do Sul:** Sao Luiz-Caaro, *Buck 11356* (LIL); Sao Salvador, Santo Inacio, *Henz 35695* (LIL); 20 km SE de Santa Rosa, *Lindeman 8990* (ICN); Santo Angelo, *Palacios-Cuezzo 1734* (LIL); Carazinho, *Pereira 8675* (RB); Quarai, Estancia de Jarau, *Rambo 26077* (LIL). PARAGUAY. **Misiones:** 12 km W de San Ignacio camino a Pilar, *Arbo 1885* (CTES). URUGUAY. **Artigas:** Ruta 30, Arroyo Catalán, paso Piaui, *Rosengurtt B7173* (MVFA, US).

*Ruellia hypericoides* seems closely related to *Ruellia erythropus*, but inhabits more open areas and is a more delicate herb with smaller flowers. The name *R. hypericoides* has been erroneously used by many authors to identify material of *Ruellia bulbifera* of group *Ebracteolati*. *Ruellia bulbifera* differs by the robust, tuberculate xylopodium, larger flowers with a short basal tube, and different structure of the capsule.

## Excluded Species

*Ruellia lanceolata*, *Chaetochlamys rusbyi*, and *Beloperone matthewsii* are different names for the same species, all based on different types. The genus in which this species should be placed is *Justicia*, and the correct name for it is *Justicia rusbyi*.

**Justicia rusbyi** (Lindau) V. A. W. Graham, Kew Bull. 43(4): 605. 1988, not *Justicia lanceolata* (Chapman) Small, 1933. *Chaetochlamys rusbyi* Lindau, Bull. Herb. Boissier 3: 491. 1895. TYPE: Bolivia. La Paz: Guanai, *Rusby 1117* (isosyntype, BM); Santa Cruz: without locality, 380 m, *Kuntze*, 1892 (isosyntype, NY).

*Ruellia lanceolata* Morong, Ann. New York Acad. Sci. 7: 193. 1893. TYPE: Paraguay. Paraguarí: Central Paraguay, between Pirayú and Jaguarón, 8 Apr. 1889. *Morong 667* (holotype, NY; isotype, US). Syn. nov.

*Beloperone matthewsii* Lindau, Bull. Herb. Boissier 6, App. 1: 30. 1898. SYNTYPE: Paraguay. Cordillera: in dumeto prope Cordillera de Altos, *Hassler 1936* (G; isosyntypes, K, P, NY).

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INDEX TO SCIENTIFIC NAMES. Accepted names in roman type, synonyms in *italics*. For explanation of names in parentheses, see under III. Group Hygrophiloidei (p. 820).

*Aphragmia* Nees ..... 798
*haenkei* Nees ..... 798
*Arrhostoxylum* Nees ..... 798, 800
*ciliatiflorum* (Hook.) Nees ..... 810
*elegans* (Poiret) Bremek. ..... 800
*formosum* (Andr.) Nees ..... 800
*glabrum* Nees ..... 798, 800
*kuntzei* (Lindau) Bremek. ..... 808
*microphyllum* Nees ..... 812
*silvaccola* var. *montanum* Nees ..... 800
*Beloperone matthewsii* Lindau ..... 842
*Blechum* Nees subgen. *Chiloblechum* Oersted ..... 798, 836
*mexicanum* Oersted ..... 836, 838
*tweedii* Nees ..... 838
*Chaetochlamys rusbyi* Lindau ..... 842
*Copioglossa* Miers ..... 798, 830
*pilosa* Miers ..... 798, 830, 833
*Cryphiacanthus* Nees ..... 798, 810
*acaulis* Nees ..... 819
*angustifolius* Nees ..... 812
*barbadensis* Nees ..... 798, 810
*udus* Nees ..... 817
*Cyrthacanthus corymbosus* Martius ex Nees ..... 804
*Dipteracanthus* Nees ..... 798, 822
(*Hygrophiloidei*) Nees ..... 820
(*Calycosi*) Nees ..... 822
(Genuini: *Bracteolati*) Nees ..... 822
(Genuini: *Ebracteolati*) Nees ..... 830
*angustifolius* ..... 833
*brachysiphon* Nees ..... 822
*brevicaulis* Nees ..... 824
*calvescens* Nees ..... 828
*canescens* Nees ..... 833
*dissitifolius* Nees var. *humilior* Nees ..... 824
*geminiflorus* (HBK) Nees ..... 831
var. *angustifolius* Nees ..... 833
var. *erectus* Nees ..... 833
var. *hirsutior* Nees ..... 833
var. *procumbens* Nees ..... 831
var. *subacaulis* Nees ..... 833
*glanduloso-punctatus* Nees ..... 828
*humilis* Nees ..... 833
*humilis* var. *minor* Nees ..... 833
*hypericoides* Nees ..... 840
*lamiiformis* Nees ..... 820
*multifolius* Nees ..... 826
*porrigens* Nees ..... 833
*porrigens* var. *triflorus* Nees ..... 833
*prostratus* Nees ..... 798, 822
*schauerianus* Nees ..... 828
*tuberosus* Nees ..... 830
*vindex* Nees ..... 833
*viscossisimus* Nees ..... 828
*Echinacanthus dichotomus* Kuntze ..... 802
*Eurychanes* Nees ..... 798
*verbasciformis* Nees ..... 798
*Gymnacanthus* Nees ..... 798, 822
*petiolaris* Nees ..... 798, 822
*Gymnacanthus* Oersted ..... 798, 830
*geminiflorus* (HBK) Oersted ..... 798, 830
*Justicia lanceolata* (Chapman) Small ..... 842
rusbyi (Lindau) V.A.W. Graham ..... 842
*Lychniothyrsus hygrophilus* (C. Martius) Bremek. ..... 817
*Penstemonacanthus* Nees ..... 798
*modestus* Nees ..... 798, 836, 838
Ruellia L. ..... 798
Group Chiloblechum ..... 836
Group Dipteracanthus ..... 822
Group Ebracteolati ..... 830
Group Hygrophiloidei ..... 820
Group Physiruellia ..... 800
Group Ruellia ..... 810
Group Salpingacanthus ..... 836
Sect. *Dipteracanthus* (Nees) Lindau ..... 822
Sect. *Euruellia* Lindau ..... 810
Sect. *Physiruellia* Lindau ..... 800
Ser. *Eglandulosae* Lindau ..... 800
*acaulis* R. Br. ..... 819
*acutangula* Nees ..... 800
*amoena* Nees ..... 804
angustiflora (Nees) Lindau ex Rambo ..... 804
*angustifolia* Swartz ..... 812
brachysiphon (Nees) Lindau ..... 822
brevicaulis (Nees) Lindau ..... 824
brevifolia (Pohl) Ezcurra ..... 802
bulbifera Lindau ..... 830
*calvescens* (Nees) Lindau ..... 828
*canescens* (Nees) Lindau ..... 833
ciliatiflora Hook. ..... 810
coerulea Morong ..... 812
coerulea Morong × brevicaulis (Nees) Lindau ..... 814
*dichotoma* Sessé & Moc. ..... 802
*dissitifolia* (Nees) Hieron. ..... 826
elegans Poiret ..... 800
epallocaulos Leonard ex Ezcurra ..... 820
erythropus (Nees) Lindau ..... 838
*formosa* Andr. ..... 800

*formosa* HBK ..... 800
geminiflora HBK ..... 830, 831
*glanduloso-punctata* (Nees) Lindau ..... 828
*graecizans* Backer ..... 802
*hirsuta* Vell. ..... 833
hygrophila C. Martius ..... 817
hypericoides (Nees) Lindau ..... 840
*ignorantiae* Herter ..... 812
kleinii Ezcurra & Wasshausen ..... 822
*kuntzei* Lindau ..... 808
*lanceolata* Morong ..... 842
*lilacina* Hook. ..... 830
*lindmaniana* Fritsch ..... 833
*loefgrenii* Lindau ..... 830
*longifolia* (Pohl) Griseb. ..... 802
longipedunculata Lindau ..... 806
longipedunculata Lindau × brevifolia (Pohl) Ezcurra ..... 808
*lorentziana* Griseb. ..... 810
macrosolen Lillo ex Ezcurra ..... 815
magniflora Ezcurra ..... 835
*matogrossensis* Lindau ..... 838
*microphylla* (Nees) Lindau ..... 812
morongii Britton ..... 819
multifolia (Nees) Lindau ..... 826
var. viscossisima (Nees) Ezcurra ..... 828
nobilis (S. Moore) Lindau ..... 836
*pubiflora* Griseb. ..... 838
reitzii Wasshausen & Smith ..... 802
sanguinea Griseb. ..... 808
*sceptrum-marianum* (Vell.) Stearn ..... 800
*serratitheca* Rusby ..... 802
solitaria Vell. ..... 828
*spectabilis* Britton ..... 812
tuberosa L. ..... 798, 810
*tweediana* Griseb. ex Fernald ..... 812
*tweedii* (Nees) T. Anderson ex Morong & Britton ..... 838
*velascana* Lindau ..... 838
*ventricosa* HBK ..... 802
*viscossisima* (Nees) Lindau ..... 828
*Salpingacanthus* S. Moore ..... 798, 836
*nobilis* S. Moore ..... 798, 836
*Sclerocalyx* Nees ..... 798
*mexicanus* Nees ..... 798
*Scordoxylum* Nees ..... 798, 800
*hartwegianum* Nees ..... 798, 800
*Siphonacanthus* Nees ..... 798, 822
*erythropus* Nees ..... 838
*villosus* Nees ..... 798, 822
*Sphingiphila tetramera* Gentry ..... 836
*Stemonacanthus* Nees ..... 798, 800
*salviaefolius* Nees ..... 798, 800
*Stephanophysum* Pohl ..... 798, 800
*angustiflorum* Nees ..... 804
*brevifolium* Pohl ..... 802
*brookeae* Bremek. ..... 806
*longifolium* Pohl ..... 798, 800
*macrandrum* Bremek. ..... 802
*ventricosum* (HBK) Nees ..... 802
*Tremacanthus* S. Moore ..... 798, 830
*roberti* S. Moore ..... 798, 830
*Ulleria* Bremek. ..... 798, 830
*geminiflora* (HBK) Bremek. ..... 798, 830

# ENDEMIC HERBACEOUS BAMBOO GENERA OF CUBA (POACEAE: BAMBUSOIDEAE: OLYREAE)[1]

*Fernando O. Zuloaga,*[2] *Osvaldo Morrone,*[2] *and Emmet J. Judziewicz*[3]

ABSTRACT

A morphological, anatomical, and taxonomic study of the endemic herbaceous bamboo (Poaceae: Bambusoideae: Olyreae) genera *Ekmanochloa* and *Mniochloa* (including its new segregate *Piresiella*) is presented; the new combination *Piresiella strephioides* is proposed. An unusual feature of all three genera is the presence of inflorescences consisting of paired, conjugate racemes. Illustrations of the leaf blade anatomy show unusual features such as the absence of fusoid cells in *Ekmanochloa* and *Mniochloa* and the presence of compound epidermal papillae in *Ekmanochloa*. The three genera are compared with possible close relatives within the Olyreae.

Cuba has a rich grass (Poaceae) flora numbering at least 400 species, with 69 of these endemic (López Almiral et al., 1989). There are four endemic genera: *Lepturidium* Hitchc. & E. Ekman (Cynodonteae), *Triscenia* Griseb. (Paniceae), and the herbaceous bamboo (Bambusoideae) genera *Mniochloa* Chase and *Ekmanochloa* Hitchc. The latter two taxa are the only endemic bambusoid genera in the entire West Indies and each is known from only a few old collections. Habitats include pine woodlands, streambanks, and limestone cliffs in the provinces of Habana and Pinar del Río (one species) and Oriente (the other three species), including serpentine outcrops. In this regard, it is noteworthy that Brooks (1987) reports 511 endemic serpentine vascular plant species for Cuba. As part of a long-term project, the goal of which is to monograph all New World bamboo genera, the following study of the morphology, anatomy, and taxonomy of these endemic "dwarf bamboos" is presented.

*Mniochloa*, named for its resemblance to the moss genus *Mnium* L., was established by Chase (1908) on the basis of two species that were described in the previous century in the genera *Olyra* L. and *Digitaria* Haller. She included the group in the Paniceae, while later authors placed *Mniochloa* in the Olyreae within the Pooideae (Hubbard, 1934), or in the Phareae (along with other herbaceous bamboos) within the Panicoideae (Bews, 1929; Roshevits, 1937). Recent authors, starting with Calderón & Soderstrom (1967), have all placed *Mniochloa* (and *Ekmanochloa*) in the Olyreae within the Bambusoideae (Calderón & Soderstrom, 1980; Clayton & Renvoize, 1986; Soderstrom & Ellis, 1987; Soderstrom et al., 1988; Watson & Dalwitz, 1988). Both *M. pulchella* (Griseb.) Chase and *M. strephioides* (Griseb.) Chase are small, delicate, trailing, almost mosslike grasses that are reminiscent of the South American olyroid genus *Raddiella* Swallen, or, because of the dimorphic culms with lax, trailing flowering shoots, *Piresia* Swallen. On closer examination of the two taxa, however, we noted a number of significant differences in morphology and leaf anatomy. Except for the large, heterogeneous group *Olyra* L. (Soderstrom & Zuloaga, 1989), olyroid genera tend to have nearly identical female spikelet morphologies; however, the differences between the two *Mniochloa* species are great and include features of floret indument, stipe and apex morphology, and relative glume length. Anatomically, *M. pulchella* lacks the characteristic bambusoid fusoid cells, whereas *M. strephioides* has them. Because of these and other features (discussed in greater detail later and summarized in Tables 1 and 2), we have decided to erect the new segregate genus *Piresiella* based on *P. strephioides*. Other characters that had appeared to unite the two species are also found in more distantly related genera in the Olyreae; for

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TABLE 1. Comparison of *Mniochloa* with *Piresiella*.

| Character | *Mniochloa* | *Piresiella* |
|---|---|---|
| Morphology | | |
| Leaf blade morphology | Elliptical; base cuneate, symmetrical to slightly asymmetrical | Ovate-triangular; base truncate, strongly asymmetrical |
| Flowering culm morphology | Erect, exceeding the vegetative culms | Lax, shorter than the vegetative culms |
| Female glume morphology | Shorter than the floret, obtuse to acute | Longer than the floret, usually acute |
| Internode between female upper glume and floret | Not prominent | Prominent |
| Female floret apex | Obtuse to acute | Apiculate |
| Female floret indument | Glabrous | Densely pubescent |
| Male spikelet apex | Glabrous | Short-pilose |
| Stamen number | 3 | 2 |
| Leaf blade anatomy | | |
| Fusoid cells | Absent | Present |
| Papillae | Densely papillose throughout | Weakly papillate between stomates; otherwise smooth |
| Intercostal short cells (abaxial epidermis) | Solitary | Paired |

example, paired, conjugate racemes are found in *Ekmanochloa*; leafless flowering shoots, in all species of *Piresia* and in species of *Olyra* (*O. ecaudata* Doell and others) and *Cryptochloa* Swallen (*C. decumbens* Soderstrom); corms are found in *Rehia* Fijten.

*Ekmanochloa* (two species) was also examined in morphological and anatomical detail. Based on such distinctive features as the deciduous leaf blades, long-awned female florets, the absence of leaf blade fusoid cells, and the presence of compound epidermal papillae, we decided that a thorough study of both *E. aristata* Hitchc. and *E. subaphylla* Hitchc. might shed light on their tenuous placement in the Olyreae.

Distribution maps for all four taxa treated in this paper can be found in Soderstrom et al. (1988).

## Materials and Methods

Herbarium specimens were examined from GH, MO, NY, and US (including type fragments from other herbaria). Transverse sections of dried leaf blades were prepared after desilification in 30% hydrofluoric acid (Breakwell, 1914); the sections were then stained in safranin and fast green. Abaxial epidermal scrapes of leaf blades were prepared by removing the mesophyll and vascular tissue with a scalpel and camel hair brush following the method of Metcalfe (1960). The epidermis was then stained in safranin. The standardized terminology of Ellis (1976, 1979) was used to describe the anatomical structure of the leaves. The vouchers for this study are marked with an asterisk in the specimens examined section of the taxonomic treatment.

## Leaf Anatomy

### *MNIOCHLOA PULCHELLA*

*Leaf blade in transverse section* (Fig. 1A, B). *Outline.* Expanded, flat; arms of the lamina straight, the two halves symmetrical on either side of the median vascular bundle; thickness at midlamina 32–52 μm. *Ribs and furrows.* Adaxial and abaxial ribs and furrows indistinguishable. *Median vascular bundle.* Midrib with simple, first-order vascular bundle distinguishable structurally from other first-order vascular bundles; adaxial projections inconspicuous; abaxial projections slightly convex. *Vascular bundle arrangement.* Three first-

TABLE 2. Comparison of *Ekmanochloa*, *Mniochloa*, and *Piresiella* with putatively related genera in the Olyreae. P: panicle; R: raceme; +: present; −: absent.

| | *Arberella* | *Cryptochloa* | *Ekmanochloa* | *Mniochloa* | *Piresia* | *Piresiella* | *Rehia* |
|---|---|---|---|---|---|---|---|
| Corms present | − | − | − | + | − | + | + |
| Culms dimorphic | − | −(+) | + | + | + (− in *P. macrophylla*) | + | − |
| Floriferous culms longer than vegetative culms | | (−) | + | + | − | − | |
| Inflorescence a raceme or a panicle | P | P | R | R | P | R | P |
| Inflorescences terminal | + | + | + | + | + | + | + |
| Inflorescences axillary | + | + | − | − | − | − | − |
| Paired unisexual inflorescences | − | − | + | + | − | + | − |
| Female floret stipe | +(−) | + | − | − | − | + | − |
| Female floret indument | Pilose | Glabrous | Glabrous | Glabrous | Pilose | Pilose | Pilose |
| Female floret apex | Acute | Acute | Long-awned | Obtuse/acute | Acute | Apiculate | Acute |
| Number of stamens | 3 | 3 | 2–3 | 3 | 3 | 2 | 3 |
| Fusoid cells | + | + | − | − | + | + | ? |
| Distribution | Central and South America | Central and South America | Eastern Cuba | Eastern Cuba | South America | Western Cuba | Northern South America |
| Number of species | 7 | 8 | 2 | 1 | 4 | 1 | 1 |

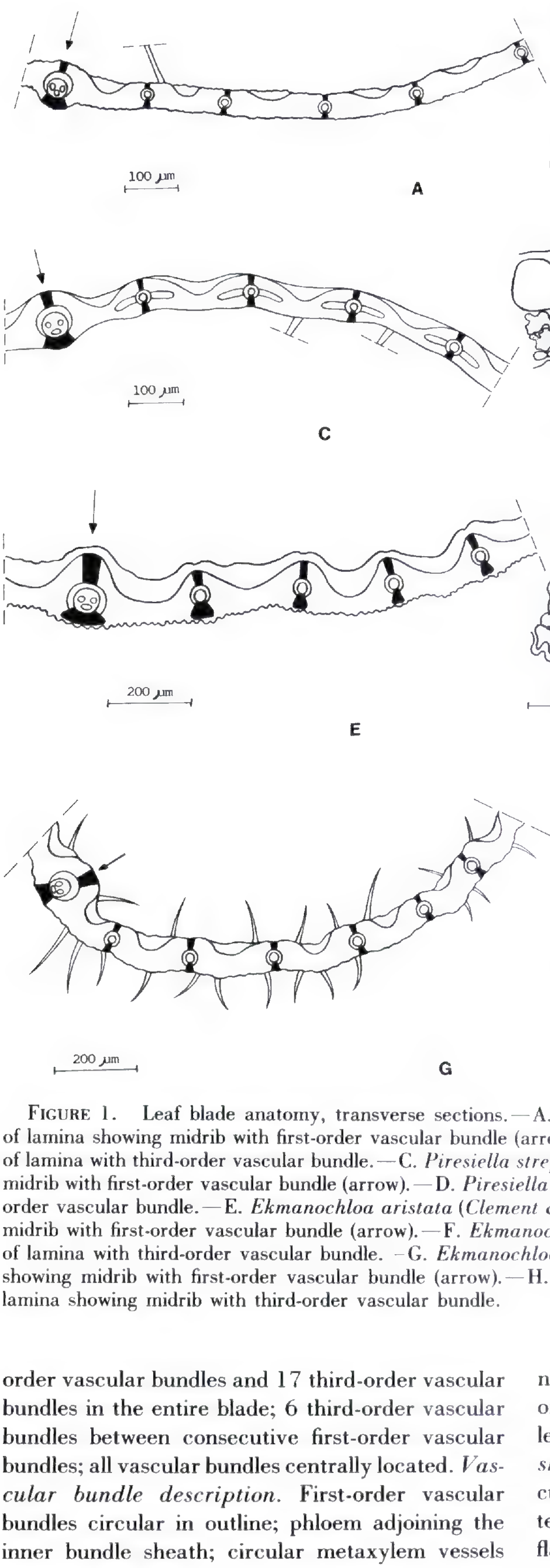
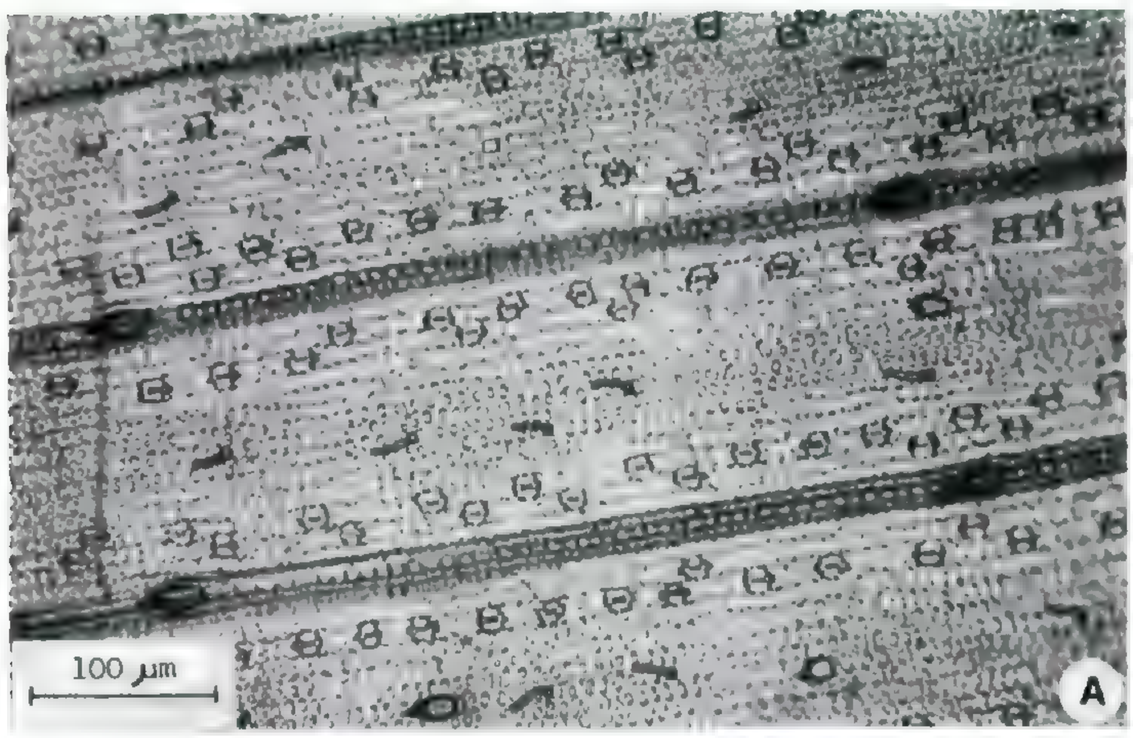
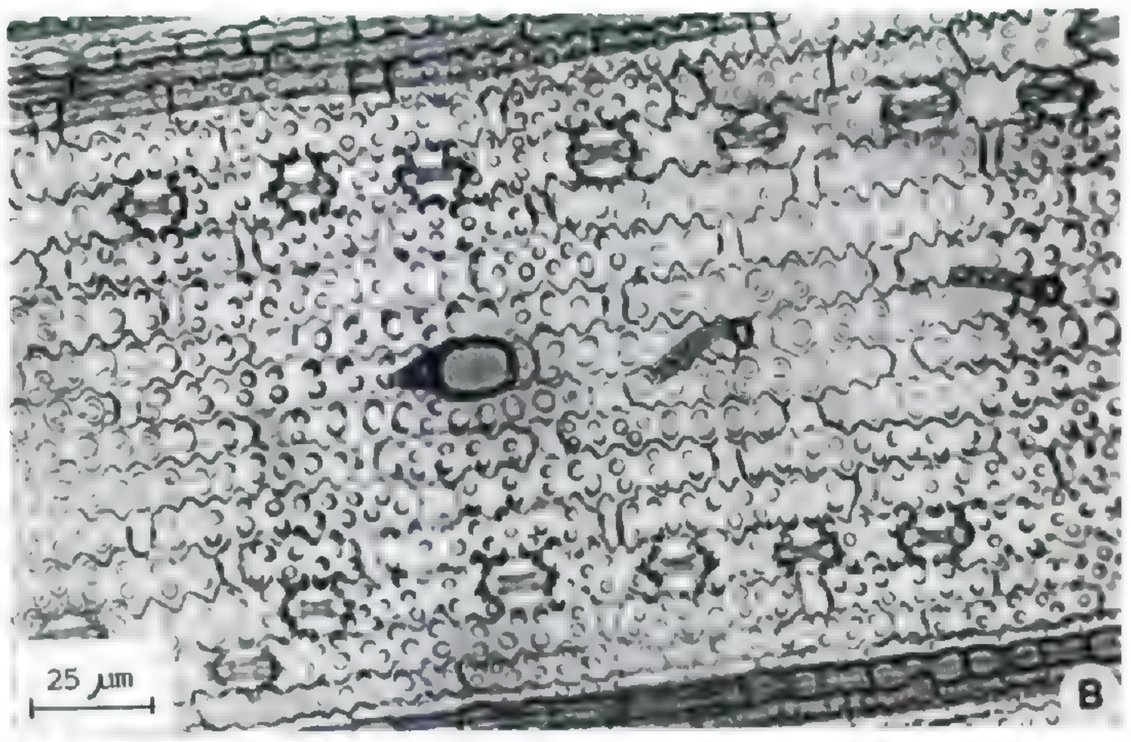
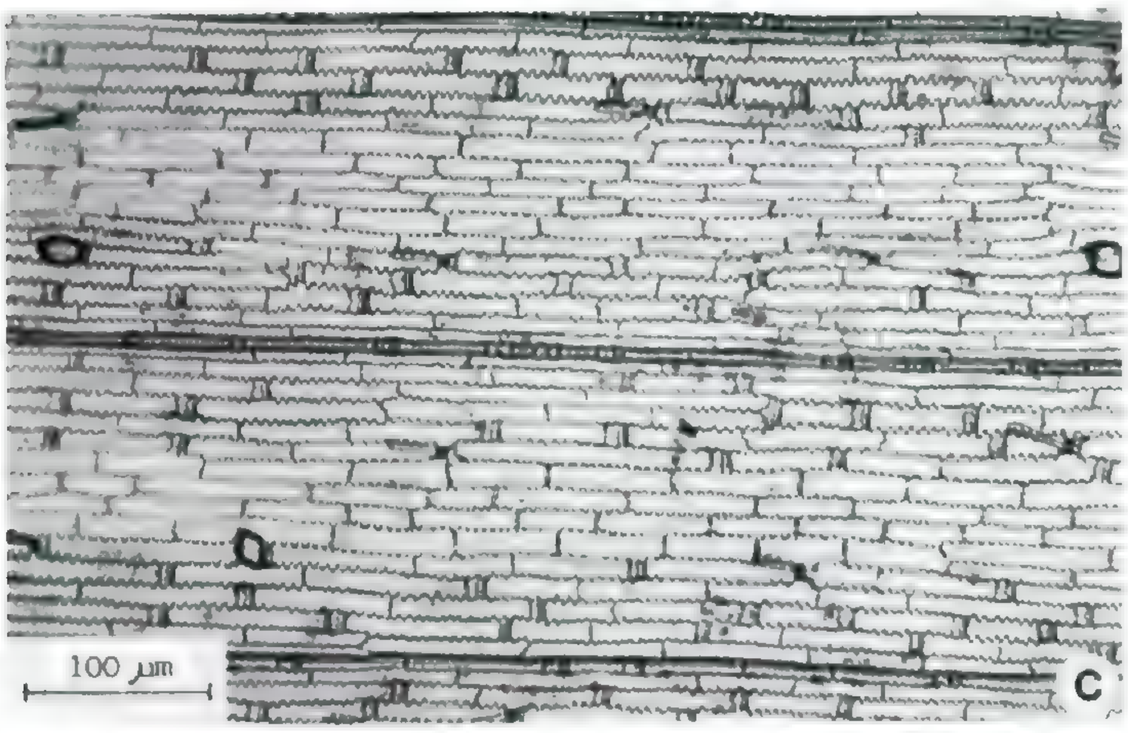


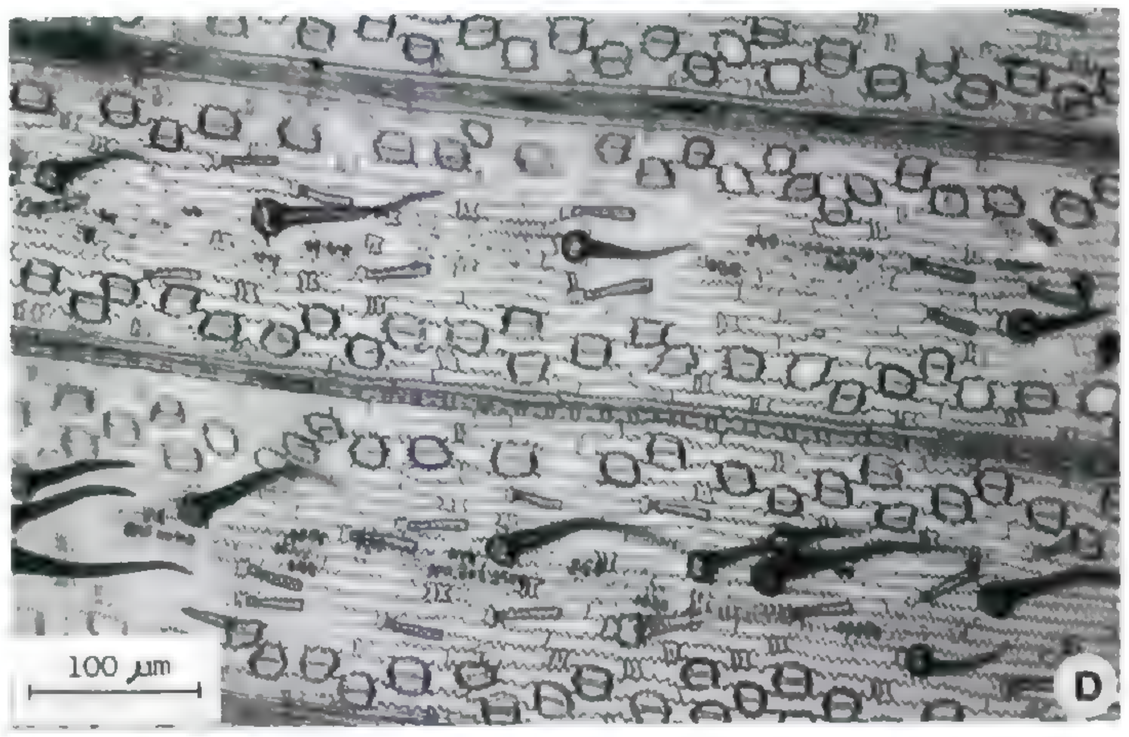

FIGURE 1. Leaf blade anatomy, transverse sections.—A. *Mniochloa pulchella* (*Wright 3448*), lateral portion of lamina showing midrib with first-order vascular bundle (arrow).—B. *Mniochloa pulchella* (*Wright 3448*), portion of lamina with third-order vascular bundle.—C. *Piresiella strephioides* (*León 4572*), lateral portion of lamina showing midrib with first-order vascular bundle (arrow).—D. *Piresiella strephioides* (*León 4572*), portion of lamina with third-order vascular bundle.—E. *Ekmanochloa aristata* (*Clement & Chrysogone 4563*), lateral portion of lamina showing midrib with first-order vascular bundle (arrow).—F. *Ekmanochloa aristata* (*Clement & Chrysogone 4563*), portion of lamina with third-order vascular bundle. –G. *Ekmanochloa subaphylla* (*Ekman 9870*), lateral portion of lamina showing midrib with first-order vascular bundle (arrow).—H. *Ekmanochloa subaphylla* (*Ekman 9870*), portion of lamina showing midrib with third-order vascular bundle.

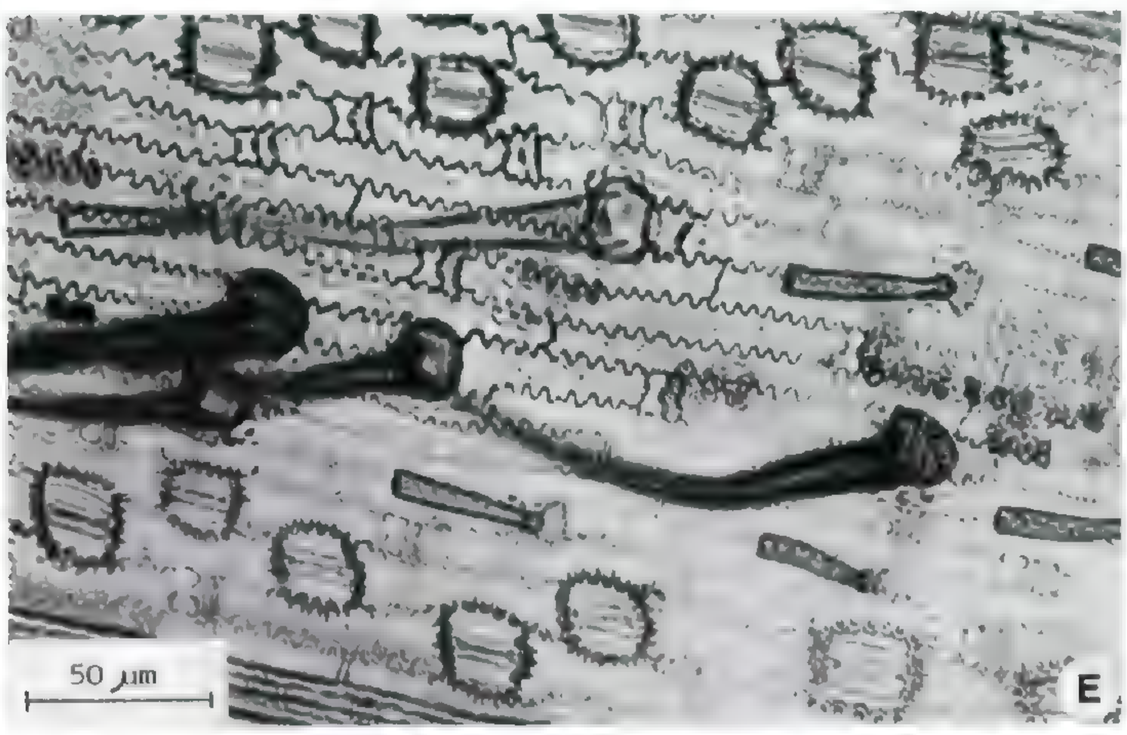
order vascular bundles and 17 third-order vascular bundles in the entire blade; 6 third-order vascular bundles between consecutive first-order vascular bundles; all vascular bundles centrally located. *Vascular bundle description.* First-order vascular bundles circular in outline; phloem adjoining the inner bundle sheath; circular metaxylem vessels narrower than the outer bundle sheath cells; third-order vascular bundles angular in outline with xylem and phloem indistinguishable. *Vascular bundle sheath.* Outer bundle sheath of the first-order vascular bundles rounded, with abaxial or adaxial interruptions, lacking extensions, comprising 6–8 inflated, rounded cells; chloroplasts absent; inner

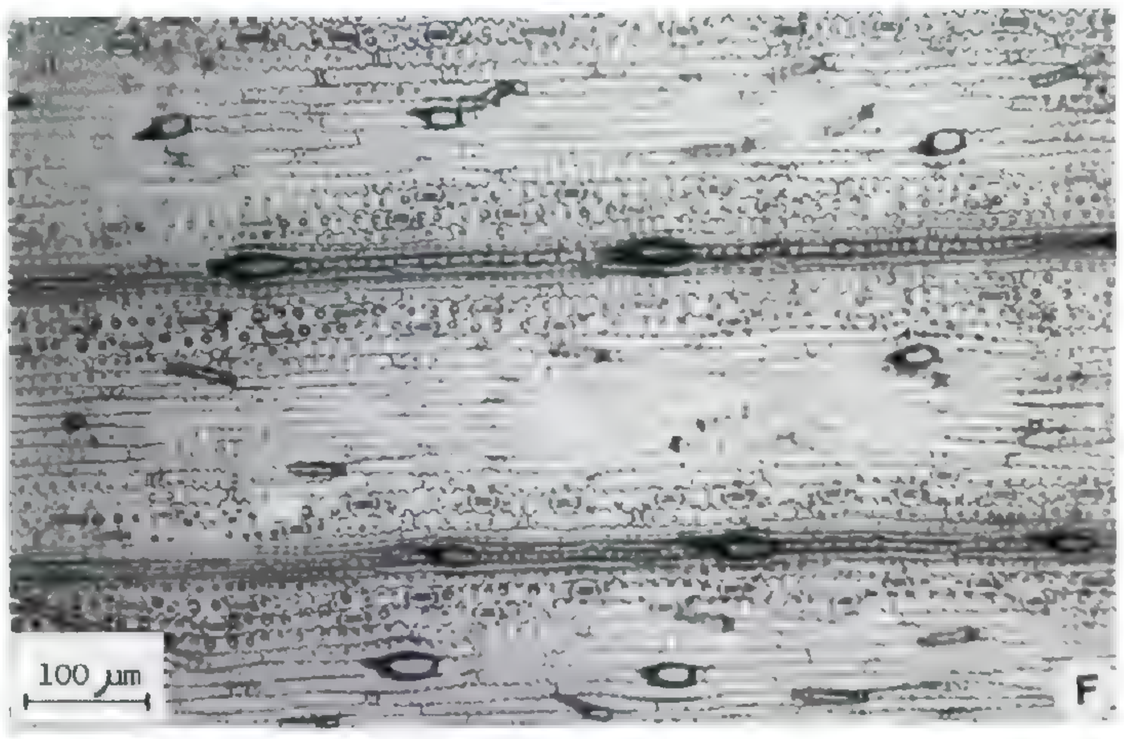


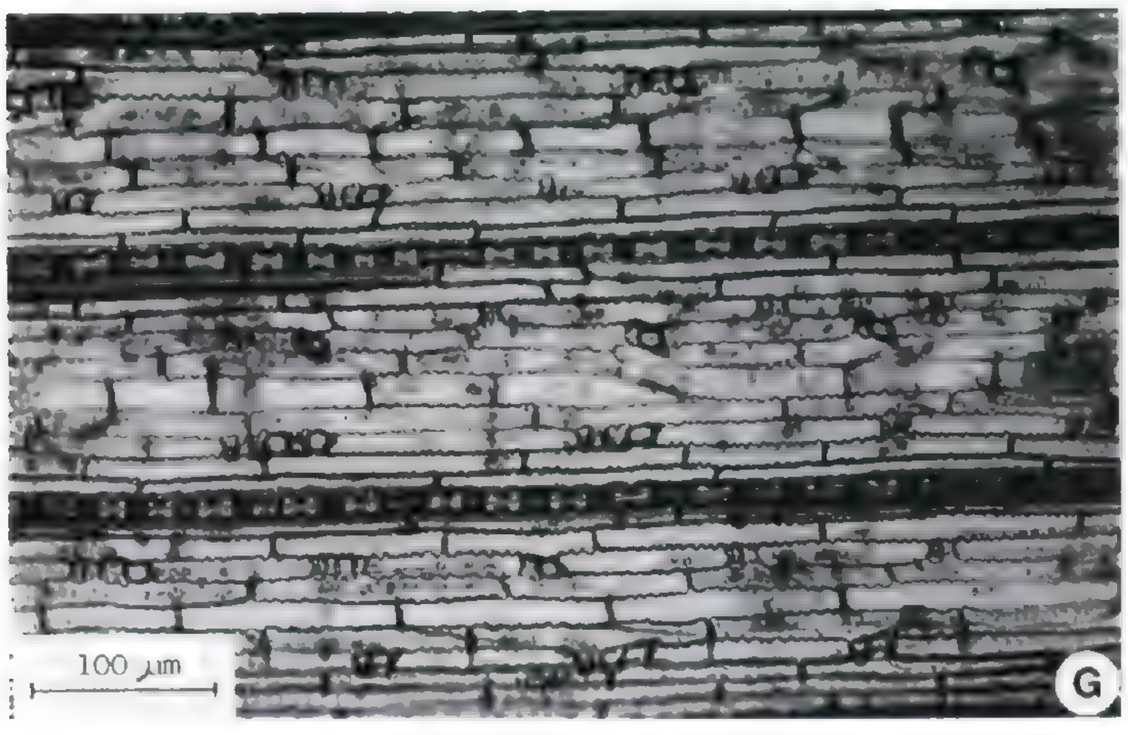



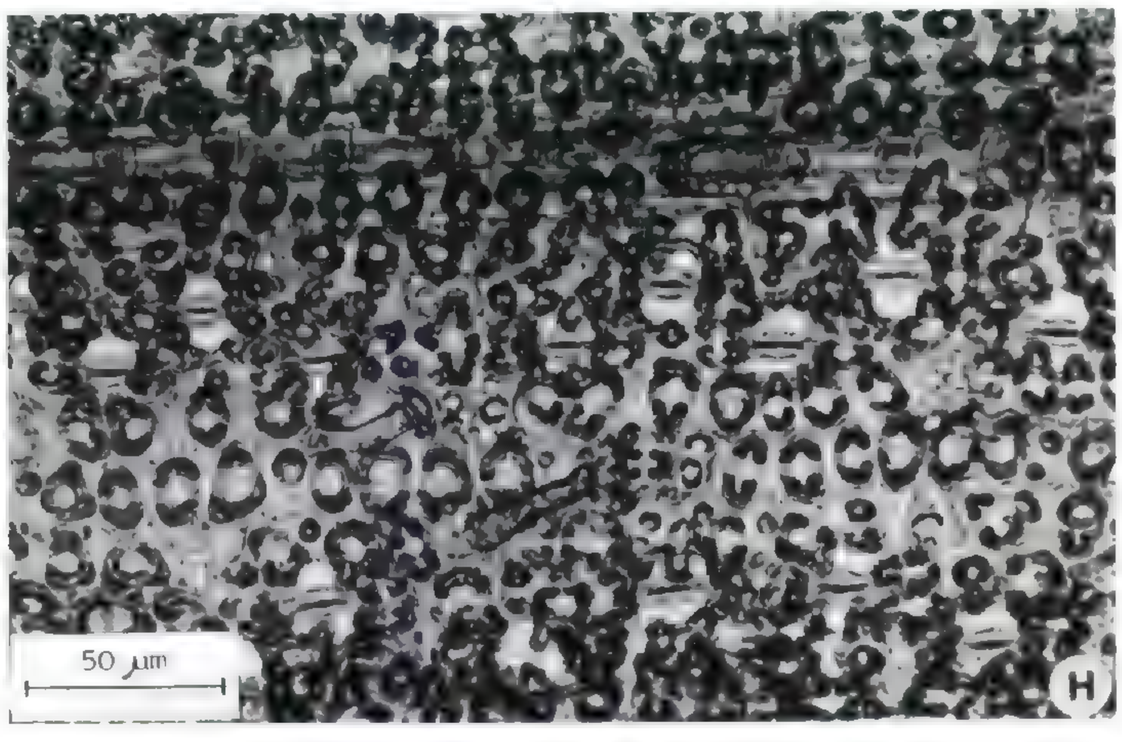




FIGURE. 2. Leaf blade epidermis in surface view. —A. *Mniochloa pulchella* (*Wright 3448*), abaxial epidermal zonation with regularly spaced costal zones. —B. *Mniochloa pulchella* (*Wright 3448*), detail of A with hooks, microhairs, and papillae located in costal and intercostal zones over long and short cells, usually arranged in two horizontal rows and overarching the stomates. —C. *Piresiella strephioides* (*León 4572*), adaxial epidermal zonation with regularly spaced costal zones. —D. *Piresiella strephioides* (*León 4572*), abaxial epidermal zonation, with stomata grouped in 4–6 files per intercostal zone. —E. *Piresiella strephioides* (*León 4572*), detail of D showing microhairs, macrohairs, and papillae overarching the stomates. —F. *Ekmanochloa subaphylla* (*Ekman 9870*), abaxial epidermal zonation with regularly spaced costal zones. —G. *Ekmanochloa aristata* (*Clement & Chrysogone 4563*), adaxial epidermal zonation with regularly spaced, narrow costal zones. —H. *Ekmanochloa aristata* (*Clement & Chrysogone 4563*), abaxial epidermis with papillae, microhairs, and stomata.

bundle sheath present, complete, consisting of small cells with uniformly thickened walls; outer bundle sheath of third-order vascular bundles rounded, with abaxial or adaxial interruptions, without extensions, consisting of 2–4 rounded cells; chloroplasts absent; inner bundle sheath absent or with a few cells abaxially. *Sclerenchyma*. Minute, with inconspicuous adaxial and abaxial girders associated with all vascular bundles, 1–3 cells deep; fibers lignified; small sclerenchyma cap at the margin. *Mesophyll*. Chlorenchyma not radiate but adaxially cells tending to a palisade-type arrangement, with conspicuous air spaces; arm cells present but with relatively shallow invaginations; 12–25 chlorenchyma cells between consecutive vascular bundles, which are 90–170 μm apart; fusoid cells absent; colorless cells absent. *Adaxial epidermal cells*. 2–3 bulliform cells present in restricted groups between all vascular bundles, generally with a large, fan-shaped central cell occupying up to ½ of the blade thickness; epidermal cells small, regular in size, with a distinct, continuous cuticle; macrohairs not seen; prickles present, usually located opposite the vascular bundles; papillae present, usually 2 per cell, narrower than the epidermal cells, relatively broad but not much more than ½ the width of the epidermal cells. *Abaxial epidermal cells*. Bulliform cells absent, otherwise cells similar to adaxial epidermis; macrohairs not seen, but hooks present, usually located between the vascular bundles; prickles and papillae similar to adaxial epidermis.

*Abaxial epidermis in surface view* (Fig. 2A, B). *Zonation*. Costal and intercostal zones distinguishable, the costal zone 3–5 cells wide, the intercostal zone 13–18 cells wide. *Intercostal long cells*. Elongated, rectangular, more than 3 times as long as wide; anticlinal walls parallel, undulating, unthickened; end walls vertical; long cells in a file separated by a short cell, or infrequently adjoining one another and without short cells. *Intercostal short cells*. Solitary, tall and narrow in outline, transversely elongated, the cork cells with crenate or undulating walls. *Stomatal complex*. 13–17 μm long, 10–13 μm wide, with 2–4 files of stomata per intercostal zone; a single interstomatal long cell usually present between consecutive stomata; subsidiary cells dome-shaped; interstomatal cells rectangular, with anticlinal walls undulating, the end walls concave. *Microhairs*. Elongated, fingerlike, 36–46 μm long, common in the median intercostal zone; basal cell two or more times as long as the distal cell, with parallel, thickened walls; distal cells short, very thin-walled, deciduous. *Macrohairs*. Not seen. *Hooks and prickles*. Small, shortly barbed, located in the median intercostal zone; prickles with the base as long as the stomata, the barb developed, located in the costal zone over the vascular bundles. *Papillae*. Rounded, simple, small, less than ½ the vertical width of the long cells, located in the costal and intercostal zones over long and short cells, commonly arranged so as to form a ring around each stomate. *Silica bodies*. Intercostal silica bodies absent; costal silica bodies dumbbell-shaped, horizontally elongated.

*Adaxial epidermis in surface view*. Adaxial epidermal cells similar to the abaxial surface except with: stomata infrequent; frequent intercostal paired silico-suberose short cells located near the costal zones; and intercostal silica bodies tall and narrow, elongated vertically, and irregular in outline.

*PIRESIELLA STREPHIOIDES*

*Leaf blade in transverse section* (Fig. 1C, D). *Outline*. Expanded, flat, with margins slightly recurved; arms of the lamina straight, the two halves symmetrical on either side of the median vascular bundle; thickness at mid-lamina 40–65 μm. *Ribs and furrows*. Conspicuous near the midnerve, inconspicuous in the rest of the blade. *Median vascular bundle*. Midrib with a simple first-order vascular bundle structurally distinguishable from the lateral first-order vascular bundles; adaxial and abaxial projections slightly convex. *Vascular bundle arrangement*. Six first-order vascular bundles and 30–40 third-order vascular bundles in the entire blade; (3–)5–7 third-order vascular bundles between consecutive first-order vascular bundles; all vascular bundles centrally located in the blade thickness. *Vascular bundle description*. First-order vascular bundles circular in outline; phloem tissue adjoining the inner bundle sheath; metaxylem vessel elements slightly angular in outline, equal or slightly larger than the outer bundle sheath cells as seen in section; third-order vascular bundles angular in outline with xylem and phloem indistinguishable. *Vascular bundle sheath*. Outer bundle sheath of the first-order vascular bundles consisting of 6–10 inflated cells, rounded, lacking chloroplasts, abaxially or adaxially interrupted by sclerenchyma girders, without extensions; inner bundle sheath present, complete, formed by small cells with uniformly thickened walls; outer bundle sheath of the third-order vascular bundles rounded to elliptical in outline, consisting of 5–6 rounded, elliptical cells, lacking chloroplasts, with abaxial interruptions, adaxial interruptions occasionally present, without extensions; inner bundle sheath absent or with a few cells near the phloem tissue. *Sclerenchyma*. Small, with inconspicuous adaxial

and abaxial girders associated with all vascular bundles, 2–3 cells deep; fibers lignified; sclerenchyma caps absent from margins. *Mesophyll.* Chlorenchyma not radiate, with adaxial chlorenchyma cells in a palisade-like arrangement and conspicuous air spaces; arm cells present, with short invaginations; 12–15 chlorenchyma cells between consecutive vascular bundles, which are spaced 165–235 μm apart; fusoid cells present, translucent, narrowly elongated, present on either side of each vascular bundle, or occasionally absent; fusoid cells separated by numerous chlorenchyma cells; colorless cells absent. *Abaxial epidermal cells.* 3–4 bulliform cells present in discrete, fan-shaped groups between all vascular bundles, the central cell large, inflated, and occupying up to ½ of the blade thickness; epidermal cells small, regular in size, with the cuticle continuous; macrohairs present, with a sunken base, not constricted, located at the margins; prickles not seen; hooks present, located between the vascular bundles near the margin; papillae absent. *Adaxial epidermal cells.* Bulliform cells absent; epidermal cells small, with the cuticle continuous; macrohairs similar to the ones on the abaxial surface; prickles not seen; hooks small, with a short barb, located in the intercostal zones near the margin; papillae narrower than the epidermal cells, associated with the stomata.

*Abaxial epidermis in surface view* (Fig. 2D, E). *Zonation.* Costal and intercostal zones distinguishable; costal zones 1–4 cells wide; intercostal zones 13–18 cells wide. *Intercostal long cells.* Long cells in files separated by pairs of short cells, elongated, rectangular, more than 5 times as long as wide, the anticlinal walls parallel and undulating, the end walls vertical. *Intercostal short cells.* In silico-suberose pairs, tall, transversely elongated; cork cells with crenate walls. *Stomatal complex.* 19–26 μm long, 11–16 μm wide, with 4–6 files of stomata per intercostal zone; a single interstomatal long cell between consecutive stomata; subsidiary cells dome-shaped or parallel-sided; interstomatal long cells rectangular, 2–3 times as long as wide, with undulating anticlinal walls and concave end walls. *Microhairs.* Located in central intercostal zone; 49–75 μm long, elongated, fingerlike, the basal cell equal to or up to twice as long as the distal cell, with parallel, thickened walls; distal cell with very thin walls, deciduous. *Macrohairs.* Located near the margins. *Hooks and prickles.* Not seen. *Papillae.* Present, associated with intercostal long cells, arranged so as to form a ring around each stomate. *Silica bodies.* Intercostal silica bodies tall and narrow, transversely elongated, irregular in outline or cross-shaped; costal silica bodies dumbbell-shaped, horizontally elongated.

*Adaxial epidermis in surface view* (Fig. 2C). Epidermal cells similar to the abaxial surface but with paired, isolated intercostal short cells; stomata not seen; hooks small, with a short barb, located in the intercostal zones near the margins; papillae absent.



*Leaf blade in transverse section* (Fig. 1E–H). *Outline.* Open, broadly V-shaped; arms of the lamina outwardly bowed, the two halves symmetrical on either side of the median vascular bundle; thickness at mid-lamina 60–130 μm (100–130 μm in *E. aristata* and 60–80 μm in *E. subaphylla*). *Ribs and furrows.* Adaxial ribs and furrows slightly developed and abaxial ribs and furrows indistinguishable in *E. aristata*; both adaxial and abaxial ribs and furrows indistinguishable in *E. subaphylla*. *Median vascular bundle.* Midrib with simple first-order vascular bundles distinguishable structurally from lateral first-order vascular bundles; adaxial projections slightly rounded, the abaxial projections not developed. *Vascular bundle arrangement.* Three first-order vascular bundles and 7–8 third-order vascular bundles in section; 5 third-order bundles; all vascular bundles centrally located in the blade in *E. subaphylla* and slightly abaxially located in *E. aristata*. *Vascular bundle description.* First-order vascular bundles circular in outline, the phloem adjoining the inner bundle sheath; metaxylem vessels narrower than the outer bundle sheath cells as seen in section; third-order vascular bundles angular or circular in outline, the xylem and phloem indistinguishable. *Vascular bundle sheath.* Outer bundle sheath of the first-order vascular bundles rounded, with 6–9 inflated, rounded or slightly elliptical cells, without extensions, with abaxial, sometimes adaxial, sclerenchyma girders; without extensions; inner bundle sheath present, complete. Outer bundle sheath of the third-order vascular bundles rounded, with abaxial, sometimes adaxial, interruptions, without extensions, consisting of 5–7 rounded or elliptical cells; inner bundle sheath absent or present, when present with a few cells abaxially. *Sclerenchyma.* Small adaxial and abaxial girders associated with all vascular bundles, 1–3 cells deep adaxially in *E. subaphylla* and 5–10 cells deep in *E. aristata*; fibers lignified; small sclerenchyma cap at the margins. *Mesophyll.* Chlorenchyma not radiate, with ad-

axial chlorenchyma in palisadelike arrangement (*E. aristata*) or not (*E. subaphylla*), with conspicuous air spaces; arm cells present but with invaginations relatively shallow, especially in *E. subaphylla*; 9–14 chlorenchyma cells present between consecutive vascular bundles, which are spaced 100–210 μm apart; fusoid cells and colorless cells absent. *Adaxial epidermal cells.* A fan-shaped cluster of 3–6 well-developed bulliform cells present between each pair of vascular bundles, the central cell very large and inflated, occupying up to ½ of the blade thickness; epidermal cells small and regular in size in *E. subaphylla*, large and inflated in *E. aristata*; macrohairs absent in *E. aristata*, absent or present in *E. subaphylla*, when present located between the vascular bundles or above them and with a bulbous, nonconstricted base; prickles present, opposite to the vascular bundles; hooks present between vascular bundles; papillae absent. *Abaxial epidermal cells.* Bulliform cells absent; epidermal cells very large, very regular in size and shape, with a continuous cuticle; macrohairs similar to the ones of the adaxial epidermis; prickles and hooks varying considerably in their distribution; papillae one per cell, rather wide, with a bi- or multi-furcated apex.

*Abaxial epidermis in surface view* (Fig. 2F, H). *Zonation.* Costal and intercostal zones distinguishable; costal zones 1–4 cells wide, the intercostal zones 13–22 cells wide. *Intercostal long cells.* In files, usually separated by paired short cells; elongated, rectangular, more than 5 times as long as wide; side walls parallel; end walls vertical; anticlinal walls undulating. *Intercostal short cells.* In silica-suberose pairs; tall, elongated, vertical; cork cells with crenate walls. *Stomatal complex.* 19–26 μm long, 19–22 μm wide, with 4–6 files of stomata per intercostal zone; a single interstomatal cell between consecutive stomates; subsidiary cells dome-shaped, triangular or parallel-sided; interstomatal long cells rectangular, with undulating anticlinal walls and concave end walls. *Microhairs.* Located in central intercostal zones; 49–59 μm long, fingerlike in *E. subaphylla* and slightly clavate in *A. aristata*; basal cell 2–3 times longer than distal cell, with thickened and parallel walls in *E. subaphylla* but with thin walls and inflated in *E. aristata*; distal cells short, with very thin walls, deciduous. *Macrohairs.* Absent in *E. aristata*; absent or present in *E. subaphylla*, when present unicellular, hard, and with a sunken base embedded in the epidermal cells. *Hooks and prickles.* Irregularly distributed and few in number. *Papillae.* Located in both the costal and intercostal zones over both long and short cells, arranged in a single horizontal row and overarching the stomates; large, more than ½ the vertical width of the long cells, with bifurcating apices. *Silica bodies.* Intercostal silica bodies tall, elongated vertically, irregular in outline, occasionally cross- or dumbbell-shaped; costal silica bodies dumbbell-shaped, horizontally elongated in *E. subaphylla* and slightly cross-shaped in *E. aristata.*

*Adaxial epidermis in surface view* (Fig. 2G). Adaxial epidermal cells similar to the ones of the abaxial surface but without papillae and isolated stomata; costal silica bodies dumbbell-shaped in *E. aristata.*

## Discussion

*Mniochloa* and *Piresiella* are $C_3$ plants with nonradiate mesophyll, parenchyma cells without specialized chloroplasts, and adjacent vascular bundles separated by more than three chlorenchyma cells. These anatomical characters are in agreement with data previously presented by Brown (1977) concerning the $^{13}C/^{12}C$ ratio for *Piresiella* (as *Mniochloa strephioides*). Anatomically, bamboos have been characterized by their possession of arm cells and fusoid cells in the mesophyll (Metcalfe, 1960; Renvoize, 1985; Soderstrom & Ellis, 1987). Both *Mniochloa* and *Piresiella* have arm cells whose walls have shallow invaginations (Fig. 1B, D). *Piresiella* has long, narrow fusoid cells on both sides of the vascular bundles, in agreement with data presented by Renvoize (1985) and Watson & Dallwitz (1988, 1992), whereas *M. pulchella* lacks fusoids. In olyroid bamboo genera the absence of fusoid cells has been previously noted in *Ekmanochloa* and *Raddiella* Swallen (Calderón & Soderstrom, 1967; Renvoize, 1985; Watson & Dallwitz, 1988, 1992); and fusoids also appear to be absent from the leaf blades of *Parodiolyra ramossisima* (Trin.) Soderstrom & Zuloaga. Soderstrom & Ellis (1987) characterized the Olyreae as having a midrib with a first-order vascular bundle associated with an adaxial projection: in *Mniochloa* and *Piresiella* the midnerve is represented by a midrib with a solitary first-order vascular bundle and the adaxial projection is absent in *Mniochloa* and only slightly pronounced in *Piresiella.*

The epidermides of *Mniochloa* and *Piresiella* are typical of the Olyreae, having rectangular long cells with undulating walls and silica bodies of the typical olyroid type. The abaxial epidermis of *Mniochloa* has solitary short cells that are suberose and transversely elongated with crenate walls. *Piresiella* has an abaxial epidermis with pairs of silica-

suberose short cells having silica bodies of the typical olyroid type. The costal silica bodies in both genera are of the short-saddle-shaped type common in the tribe. Epidermal papillae are frequent in the Olyreae (Calderón & Soderstrom, 1967; Renvoize, 1985; Soderstrom & Ellis, 1987). *Mniochloa* has small, simple papillae distributed in longitudinal files associated with long and short cells on both epidermides and also bordering the stomatal apparatuses. Watson & Dallwitz (1988), in their description of *Mniochloa* (without citing a voucher or the species studied), noted the absence of fusoid cells; this is an obvious reference to *Mniochloa pulchella*, whereas their observation of the presence of papillae only in the vicinity of the stomates must pertain to *Piresiella strephioides*. *Piresiella* possesses small, simple papillae only on the abaxial surface concentrated in the vicinity of, and slightly overarching, the stomates. The presence of papillae restricted to the stomatal area has also been noted in the Olyreae in *Reitzia* Swallen (Calderón & Soderstrom, 1967).

*Ekmanochloa* includes $C_3$ species with nonradiate mesophyll, with cells of the outer bundle sheath lacking specialized chloroplasts, and with more than three cells between adjacent vascular bundles. In transverse section the mesophyll has chlorenchyma cells with invaginated walls, as is characteristic of the bamboos. However, fusoid cells are absent from the mesophyll, in agreement with the reports of Calderón & Soderstrom (1967), Renvoize (1985), and Watson & Dallwitz (1988, 1992). The epidermis of *Ekmanochloa* is typical of herbaceous bamboos, having rectangular long cells with undulating walls, short cells in silico-suberose pairs, and the cork cells vertically elongated with crenate walls. The silica bodies are saddle-shaped, although in *E. aristata* the costal silica bodies are slightly cruciform. The presence of cross-shaped costal silica bodies has been previously noted in *Piresia* (Calderón & Soderstrom, 1967) and in *Piresia* and *Rehia* Fijten (Watson & Dallwitz, 1988, 1992). Calderón & Soderstrom (1967) noted in *Ekmanochloa* the presence of costal silica bodies with transitional forms to silica bodies more typical of those of the Oryzeae; in the present study these transitional forms were not observed. The presence of large, compound papillae on the abaxial epidermis, distributed in a file among the long and short cells and overarching the stomatal apparatus, is characteristic of *Ekmanochloa*. The presence of compound papillae in the Olyreae has otherwise been noted only in *Piresia* (Calderón & Soderstrom, 1967) and, perhaps more weakly so, in *Maclurolyra* Calderón & Soderstrom (Calderón & Soderstrom, 1973; Renvoize, 1985).

The two species of *Ekmanochloa* have bicellular microhairs with quite different morphologies. In *E. aristata* the microhairs (barely visible in Fig. 2H) are claviform or obconic, with the walls of the basal cell not parallel, and the distal cell very short in relation to the basal cell. In *E. subaphylla* (Fig. 2F) the microhairs are narrow, fingerlike, and have the distal cell only slightly shorter than the basal cell, as in most olyroids. In comparison to *E. subaphylla*, in transverse section the blades of *E. aristata* are narrower, and the vascular bundles are slightly displaced toward the abaxial epidermis and associated with deep columns of sclerenchyma cells.

## Taxonomic Treatment

**Mniochloa** Chase, Proc. Biol. Soc. Wash. 21: 185. 1908. TYPE: *Mniochloa pulchella* (Griseb.) Chase (designated by Chase, 1908).

Delicate, tufted, monoecious perennial from small corms. Culms weak, straggling, dimorphic (vegetative and leafless flowering). Vegetative culms with several fully developed leaves per complement; ligules inconspicuous; pseudopetioles short; blades elliptical, symmetrical to slightly asymmetrical. Flowering culms erect, usually much exceeding the leaves, with only bladeless sheaths. Racemes 2, conjugate, erect, appressed, subequal, unisexual. Female racemes slightly longer than the male racemes, with several spikelets on short, slightly clavate pedicels. Female spikelets 1-flowered, narrowly ellipsoidal, falling entire; glumes delicately membranous, distinctly shorter than the floret, ovate-elliptical, 3-nerved, glabrous, obtuse to acute, the margins scabrous, the lower glume slightly shorter than the upper; internode between upper glume and floret inconspicuous; floret fusoid to narrowly ellipsoid, acute to obtuse, membranous, glabrous, pale; lemma 3-nerved; palea about as long as the lemma; lodicules 3, small; gynoecium not seen. Male racemes with several spikelets on short, slightly clavate pedicels. Male spikelets 1-flowered, much shorter than the female spikelets, lacking glumes, ellipsoid, acute; lemma 1-nerved; palea 2-nerved, with apex obtuse; stamens 3. Caryopsis fusoid; hilum linear, extending nearly the full length of the caryopsis, from slightly above the base to nearly the apex; embryo small, basal. Chromosome number unknown.

*Distribution.* A monotypic genus of limestone cliffs in lowland Oriente, Cuba.

**Mniochloa pulchella** (Griseb.) Chase, Proc. Biol. Soc. Wash. 21: 186, pl. 4. 1908. *Digitaria pulchella* Griseb., Cat. Pl. Cub. 231. 1866.

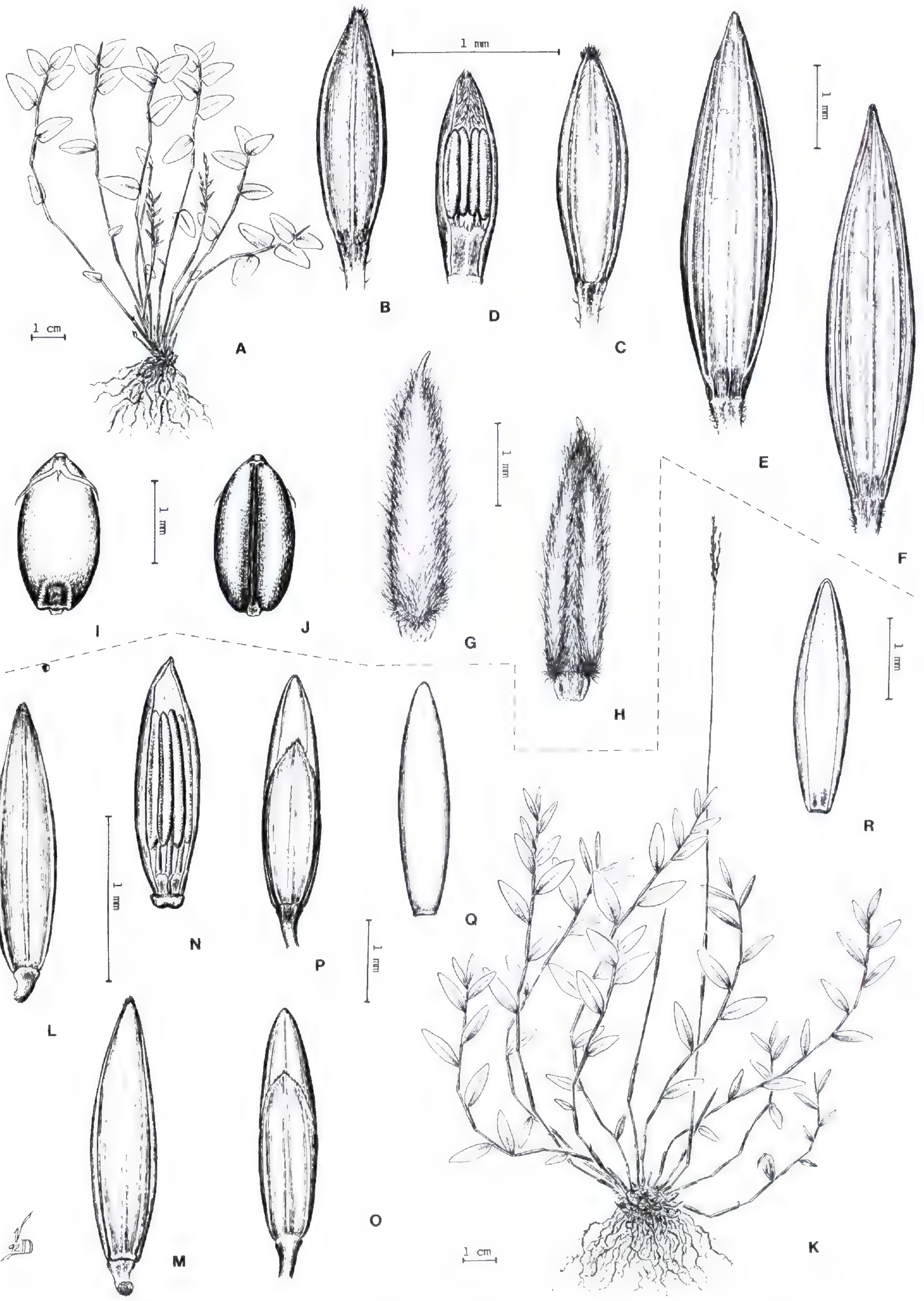



FIGURE 3. A–J, *Piresiella strephioides* (Griseb.) Judziewicz, Zuloaga, & Morrone (A, I–J from *León 4572*; B H from *Wright 3435*).—A. Habit. B–D, male spikelet: B. Lemma view.—C. Palea view. D. Palea and two stamens. E–H, female spikelet: -E. Upper glume view.—F. Lower glume view. G. Floret, lemma view. H. Floret, palea view.—I, J. Caryopsis, embryo and hilum views. K–R, *Mniochloa pulchella* (Griseb.) Chase (K from *Ekman 3916*; L R from *Wright 3448*).—K. Habit. L–N, male spikelet:—L. Lemma view.—M. Palea view.—N. Palea and three stamens. O–R, female spikelet:—O. Upper glume view.—P. Lower glume view. Q. Floret, lemma view.—R. Floret, palea view.

*Strephium pulchellum* (Griseb.) C. Wright, Anales Acad. Ci. Méd. Habana 8: 202. 1871. TYPE: Cuba. Oriente: Yunque de Baracoa, on vertical cliffs, 8 June 1856, *C. Wright 3448** (holotype, GOET not seen; isotypes, GH, MO). Figure 3K–R.

Corms 1.5–2.5 mm diam. Vegetative culms 3–12 cm tall, 3–9 leaves per complement; sheaths 2.5–7 mm long, usually shorter than the internodes, slightly inflated, 5–7-nerved, glabrous to pubescent, the truncate summit with a few delicate marginal cilia; ligules a hyaline, lacerate, ciliate membrane 0.1 mm long; pseudopetioles 0.1–0.4 mm long, glabrous, yellowish to brownish; blades 7–15 mm long, 2–4 mm wide, obtuse and weakly apiculate at the apex, both surfaces pubescent throughout with short, appressed hairs, less commonly nearly glabrous, or the adaxial surface often with ca. 1-mm-long, straggling hairs. Flowering culms 7–20 cm long, with 1–2 bladeless sheaths; peduncle filiform, glabrous. Racemes with the rachises slender, slightly flexuous, glabrous, scaberulous. Female inflorescences 0.8–3 cm long, with (4–)8–13 spikelets on pedicels 0.2–0.5 mm long. Female spikelets 2.2–2.8 mm long; glumes greenish, ovate-elliptical, the lower 1.7–1.9 mm long, the upper 2–2.2 mm long; floret as long as spikelet; lodicules 0.2–0.3 mm long, flabellate, hyaline. Male inflorescences 0.5–2.3 cm long, with (3–)7–12 spikelets; pedicels ca. 0.2 mm long, dark-colored. Male spikelets 1.3–1.7 mm long; anthers 0.8–1 mm long, fusoid, orangish yellow when dry. Caryopsis 1.5–2 mm long, 0.5–0.6 mm wide; embryo ca. 0.4 mm long.

*Phenology.* Apparently flowering in March, June, and December.

*Distribution.* Known only from limestone cliffs in lowland Oriente, Cuba; according to L. Catasús Guerra (17 May 1982 letter to T. R. Soderstrom), the most recent collection in the HAC herbarium was made in 1960.

*Additional material examined.* CUBA. **Oriente:** Baracoa, El Yunque, on steep, shady limestone rocks, very rare, 17–18 Dec. 1914, *Ekman 3916** (US); Sierra de Moa, Cayoguán, in crevices of rocks, 30 Mar. 1942, *León 20898* (US).

**Piresiella** Judziewicz, Zuloaga, & Morrone, gen. nov. TYPE: *Piresiella strephioides* (Griseb.) Judziewicz, Zuloaga & Morrone (= *Olyra strephioides* Griseb.).

Gramina perennia humilia caespitosa. Culmi dimorphi, floriferi laxi, decumbentes, circa dimidis culmorum vegetativorum statura. Racemi bini, ascendentes, adpressi, inaequales, unisexuales. Spiculae femineae ovoideae deciduae aut glumae deciduae poster. Glumae pariter longae ac spicula; internodium inter glumam superiorem et flosculum prominens; flosculus glumis minor, albidus, tenuis, pilis adpressis, albis, sericeis, ornatus; lemma apiculatum vel cucullatum. Spiculae masculae minores foemineis glumis expertes.

Delicate, caespitose, monoecious perennials from small corms, with delicate, elongate stolons. Culms dimorphic, either vegetative or (leafless) flowering. Vegetative culms with several fully developed leaves per complement, these all near the apex; ligules minute, membranous; pseudopetioles short; blades ovate-triangular, truncate and strongly asymmetrical at the base, acute at the apex. Flowering culms lax, decumbent, about one-half as tall as the vegetative culms. Inflorescences terminal, exerted, consisting of 2 conjugate, ascending, appressed, subequal unisexual racemes. Female racemes with narrow rachises and few spikelets. Female spikelets 1-flowered, ovoid, falling entire or the glumes tardily deciduous; glumes as long as spikelet, subequal, narrowly ovate, acute to acuminate, chartaceous, 3(–5)-nerved, sulcate, glabrous; internode between upper glume and floret prominent; floret membranous, shorter than the glumes, whitish, covered with delicate, appressed, white, silky hairs; lemma and palea equal, the lemma apex apiculate or cucullate, not evidently nerved, the margins enfolding the palea; palea 2-keeled; lodicules 3, small; gynoecium with 3 stigmas. Male racemes slightly shorter than the female racemes, with slender rachises and few spikelets on short pedicels. Male spikelets 1-flowered, shorter than female spikelets, ellipsoid, glabrous, persistent, lacking glumes; lemma as long as spikelet, lanceolate-ovate; palea nearly as long as lemma; stamens 2. Caryopsis broadly ellipsoid; hilum linear, extending the full length of the caryopsis; embryo small, basal. Chromosome number unknown.

*Distribution.* A monotypic genus of ravines, palm savannas, and streambanks in lowland Habana and Pinar del Río, Cuba.

*Discussion.* This new genus shares with *Mniochloa*, *Ekmanochloa*, *Piresia*, and some species of *Cryptochloa*, *Olyra*, and *Pariana* Fusée-Aublet inflorescences on separate culms that lack fully developed leaves. It differs from all of these genera except *Mniochloa* and one species of *Ekmanochloa* in its conjugate, unisexual racemes and spikelets with two rather than three or more stamens.

*Piresiella* differs from *Mniochloa* by eight morphological and three anatomical characters given in Table 1.

The stipe of the female floret in *Piresiella* resembles elaiosomes; these have been confirmed in *Olyra obliquifolia* Steudel, *O. fasciculata* Trin., and all species of *Cryptochloa* (Davidse, 1987). This elaiosomelike resemblance is suspected in other genera such as *Froesiochloa* G. A. Black and the non-olyroid herbaceous bamboos *Anomochloa marantoidea* Brongn. and *Puelia* Franchet.

The generic name is a diminutive of *Piresia* and was suggested by the superficial resemblance (Table 2) to a small species of that genus. *Piresiella* rivals *Raddiella minima* Judziewicz & Zuloaga as the smallest of all the bambusoid grasses; some individuals with mature inflorescences have vegetative culms only 5 cm tall, with flowering culms 3 cm long.

**Piresiella strephioides** (Griseb.) Judziewicz, Zuloaga & Morrone, comb. nov. Basionym: *Olyra strephioides* Griseb., Cat. Pl. Cub. 229. 1866. *Mniochloa strephioides* (Griseb.) Chase, Proc. Biol. Soc. Wash. 21: 186. 1908. TYPE: Cuba. Pinar del Río: Río Santa burk [? spelling of last word uncertain], among the adventitious roots of palms, river margin, 27 Aug.–5 Sep. 1865, *C. Wright 3435* (holotype, GOET not seen, fragment, US; isotypes, GH, HAC not seen, MO, NY, US). Figure 3A–J.

Corms 1–2 mm diam.; stolons up to 20 cm. Vegetative shoots (7–)10–18 cm tall, with 3–7 leaves per complement; internodes pubescent in a line, otherwise glabrous; nodes often swollen, geniculate, slightly retrorsely bearded, shrinking when dry to produce a double flange; sheaths glabrous except pubescent on one margin and with a fringe of fine, excelsiorlike cilia at the summit; ligules 0.1 mm long, membranous, ciliolate; pseudopetioles 0.2–0.6 mm long, tan, glabrous; blades 14–20 mm long, 6–10 mm wide, glabrous to puberulent on both surfaces. Flowering culms each with a single bladeless sheath, this glabrous except for one pubescent margin. Racemes with the rachises slender, angled, scabrous, slightly flexuous, glabrous to pubescent. Female inflorescenes 1.5–3 cm long, with 6–9 spikelets on pedicels 0.2–0.6 mm long; rachises 0.2–0.3 mm wide. Female spikelets 4–4.8 mm long; glumes greenish or whitish (sometimes with purplish apices), with a few faint cross-nerves, spreading up to 180° at maturity; internode between upper glume and floret 0.3–0.5 mm long; floret 3–3.5 mm long, whitish; lodicules 0.7–0.8 mm long, truncate. Male racemes with the rachis ca. 0.1 mm wide, bearing 6–8 spikelets on pedicels 0.3–1.5 mm long (longest at the base of the raceme). Male spikelets 1.3–1.8 mm long; anthers 0.5–0.7 mm long, yellowish orange when dry. Caryopsis 2 mm long, 0.8 mm wide; embryo 0.2–0.3 mm long.

*Phenology.* Apparently flowering from July through November.

*Distribution.* Palm savannas, ravines, and streambanks in lowland Habana and Pinar del Río, Cuba; reported by L. Catasús Guerra as having been collected by him as recently as 1974 (17 May 1982 letter to T. R. Soderstrom).

*Additional material examined.* CUBA. **Habana:** Loma de Coca, locis perumbrosis, 2 June 1914, *Ekman 1238* (US); banks of Río Guanabo, near Campo Florida, 10 Oct. 1943, *León 4140* (US). **Pinar del Río:** hills W of Cayajabos, in forest, 25 June 1921, *Ekman 12945* (US); Cabaños, Guabal de Lechuza, 2 July 1921, *Ekman s.n., Amer. Gr. Nat. Herb. 1029** (US); first range of hills 13 km NW of Pinar del Río, 26 Nov. 1926 (sterile), *Hitchcock 23310* (US); N of San Diego de los Baños, banks of an arroyo, 18 Aug. 1914, *León & Hiram 4391* (US); ravine near La Guira, not far from San Diego de los Baños, 26 Aug. 1914, *León 4572** (US); not far from San Diego de los Baños, banks of a rivulet, at the base of a palm, 21 Aug. 1914, *León 4593* (US).

**Ekmanochloa** Hitchc., Man. Grasses W. Ind. 374. 1936. TYPE: *Ekmanochloa subaphylla* Hitchc. (designated by Hitchcock, 1936).

Caespitose, short rhizomatous, monoecious perennials from small corms. Culms erect, simple, dimorphic. Vegetative culms with 3–6 fully developed leaves per complement. Sheaths striate, glabrous or pilose in the distal portion; ligules membranous, small; pseudopetioles short; blades linear-lanceolate, flat, glabrous or short-pilose, deciduous. Flowering culms with 2–3 bladeless leaves. Inflorescence terminal, exerted, consisting of 2 conjugate, erect, appressed, subequal unisexual racemes with filiform, slightly flexuous, glabrous, smooth rachises. Female racemes slightly longer than the male racemes, of 3–5 spikelets on clavate pedicels; male inflorescences of 3–12 spikelets on slightly clavate pedicels. Female spikelets 1-flowered, narrowly ellipsoid; glumes shorter than to as long as the floret, glabrous to sparsely pilose, the lower 5-nerved, the upper 3-nerved; internode between upper glume and floret short or up to 0.5 mm, pilose; floret fusiform, membranous, obliquely inserted above the glumes, early deciduous; lemma aristate, 3–5-nerved; palea 2-nerved, the apex not enfolded by the lemma; lodicules 3, flabellate, hy-

aline; gynoecium oblong, with 2 free styles. Male racemes of 3–12 spikelets on slightly clavate pedicels. Male spikelets 1-flowered, ellipsoid, hyaline, lacking glumes; lemma 3-nerved; palea 2-nerved; lodicules 3, hyaline; stamens 2–3. Caryopsis fusiform; hilum extending the full length of the ventral side; embryo small. Chromosome number unknown.

*Distribution.* A genus of two species endemic to ultramafic (serpentine) areas in lowland Oriente, Cuba.

*Discussion.* *Ekmanochloa* differs from most of the Olyreae in the following: (1) absence of fusoid cells (but these are also lacking in some species of *Raddiella* and *Mniochloa*); (2) presence of strongly compound papillae on the abaxial epidermis (these also present in *Piresia* and *Rehia*, but not so strongly developed); (3) deciduous leaf blades; and (4) prominently long-awned female lemmas (lemma awns are found elsewhere in the tribe only in *Agnesia* Zuloaga & Judziewicz (1993) and *Piresiella*, where they are very short and may more properly be termed apiculi).

*Ekmanochloa* also shares some characters with the doubtfully olyroid, monotypic *Buergersiochloa* Pilger of New Guinea: both of these taxa have long-awned female florets, compound epidermal papillae, and dimorphic culms. However, both have many significant morphological and anatomical differences, and it does not seem likely that they are closely related.

When both species of *Ekmanochloa* are compared with other members of the Olyreae, it appears that *E. subaphylla* is more specialized than *E. aristata*. Besides its specialized limestone cliff habitat, *E. subaphylla* differs from *E. aristata* in its two rather than three stamens; very short, emarginate rather than long and entire female glumes; leaf blades with a less well-developed adaxial palisadelike chlorenchyma layer; and slightly less well-developed arm cells. Furthermore, Clayton & Renvoize (1986) noted that the leaf blades of *E. subaphylla* are more likely to be more completely suppressed than those of *E. aristata*. Another specialized feature present in *E. aristata* is microhairs with a distinctive squat, obconic basal cell. *Ekmanochloa subaphylla* has fingerlike, typically olyroid bicellular microhairs.

KEY TO THE SPECIES OF *EKMANOCHLOA*

1a. Female spikelets with glumes about as long as the body of the floret, sparsely pilose; lemma with an awn 16–18 mm long; male inflorescence with 3–4 short-pilose spikelets 2.7–3.3 mm long; stamens 3 ..... 1. *E. aristata*

1b. Female spikelets with glumes much shorter than the body of the floret, glabrous; lemma with an awn 5–10 mm long; male inflorescence with 6–12 glabrous spikelets 1.7–2.3 mm long; stamens 2 ..... 2. *E. subaphylla*

**1. Ekmanochloa aristata** Hitchc., Man. Grasses W. Ind. 377. 1936. TYPE: Cuba. Oriente: between Taco and Nibujón, in carrascales-pinales, very rare, 4 Dec. 1914, *E. L. Ekman 3729** (holotype, US; isotype, S not seen). Figure 4A–F.

Short-rhizomatous perennial. Vegetative culms 30–50 cm tall, erect, unbranched, with 3–5 fully developed leaves per complement. Leaves with sheaths 1–4 cm long, shorter than the internodes, the margins overlapping, membranous, ciliate toward the apex, otherwise glabrous; ligules 0.1–0.2 mm long, laciniate at the apex; pseudopetioles 0.3–0.6 mm long, brownish, glabrous to short-pilose; blades apparently early deciduous, 8–55 mm long, 2–4 mm wide, linear-lanceolate, narrowed and slightly asymmetrical at the base, acute at the apex, glabrous, the margins smooth, glabrous. Flowering culms 20–50 cm tall, erect, usually exceeding the vegetative culms, unbranched, with two bladeless leaves present; peduncle up to 25 cm long, filiform, glabrous. Female inflorescence 15–20 mm long, with 3–5 spikelets at a distance of 4–8 mm from each other; pedicels clavate, 3.3–5 mm long, smooth, glabrous. Female spikelets 6–9 mm long, 0.9 mm wide; glumes as long as the body of the floret, subequal, membranous, sparsely pilose with appressed hairs; internode between upper glume and floret short, pilose; floret 5–7 mm long (excluding awn), 0.6 mm wide, fusiform, acute, scaberulous, pale; lemma 3-nerved, with an awn 16–18 mm long; palea shorter than the lemma; lodicules 0.5–0.7 mm long, brownish, apically laciniate. Male inflorescence 10–15 mm long, with 3–4 spikelets; pedicels 0.6–2.5 mm long, smooth, glabrous. Male spikelets 2.7–3.3 mm long, 0.5 mm wide, acute, sparsely pilose with short, appressed hairs between the nerves; lodicules 0.5 mm long, brownish; stamens 3, the anthers 0.8 mm long. Caryopsis 4.2 mm long, fusoid, brown, the embryo ca. 0.6 mm long.

*Phenology.* Apparently flowering in March, June, and December.

*Distribution.* Rare in pine savannas in lowland Oriente, Cuba; last collected in 1945 (L. Ca-

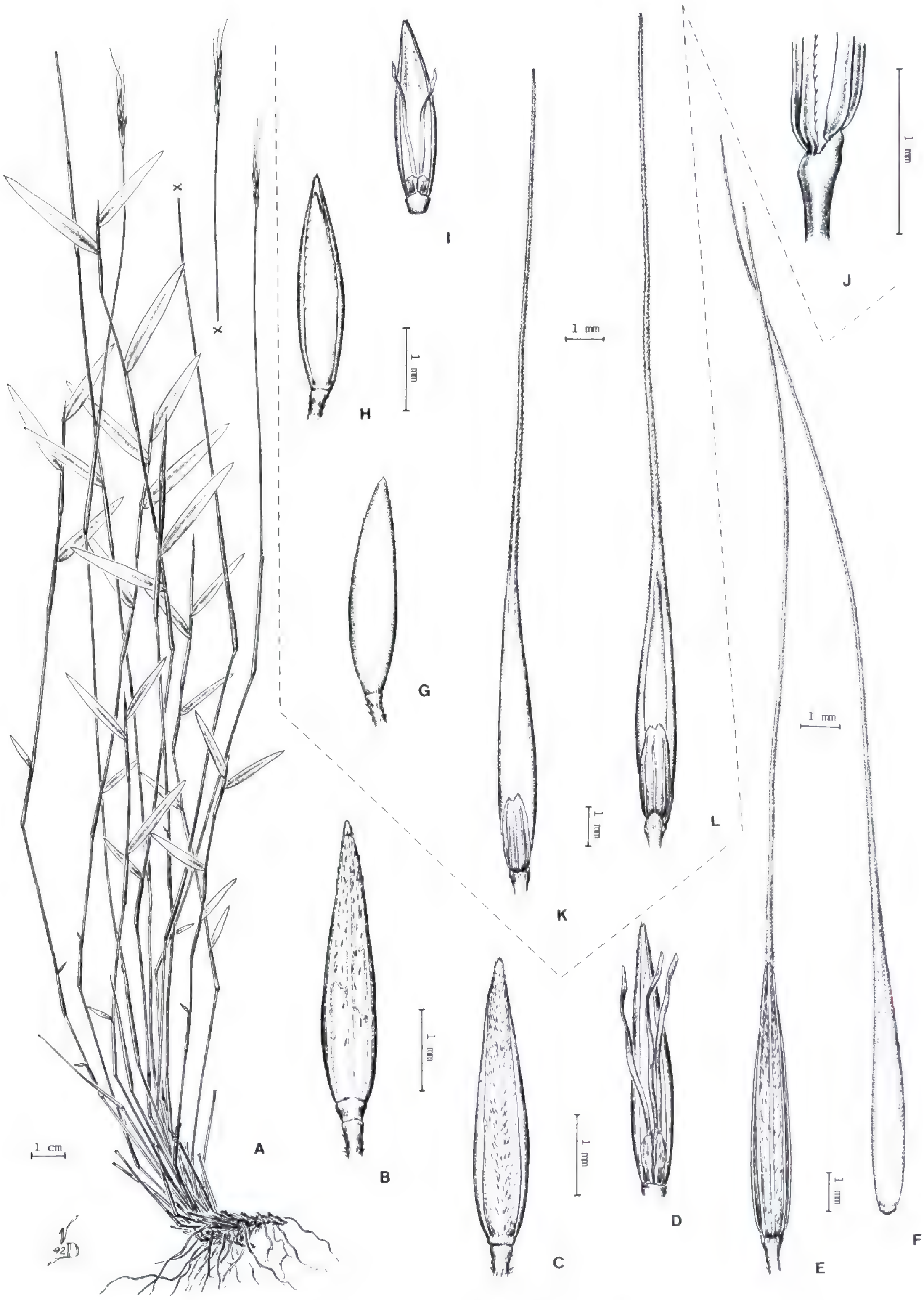



FIGURE 4. A–F, *Ekmanochloa aristata* Hitchc. (A, E, F from *Ekman 3729*; B, D from *Clement & Chrysogone 4563*).—A. Habit. B–D, male spikelet:—B. Lemma view.—C. Palea view.—D. Palea and three filaments. E–H, female spikelet:—E. Upper glume view. -F. Lower glume view. G L, *Ekmanochloa subaphylla* Hitchc. (from *Ekman 9870*). G–I, male spikelet:—G. Lemma view.—H. Palea view.—I. Palea and two filaments. J–L, female spikelet:—J. Base, lateral view.—K. Upper glume view. —L. Lower glume view.

tasús Guerra, 17 May 1982 letter to T. R. Soderstrom).

*Additional material examined.* CUBA. **Oriente:** Pineland not far from Moa airport, 26 June 1945, *Clement & Chrysogone 4563** (US); valley of the Río Cayoguán, near the mines, Moa, 30 Mar. 1942, *León et al. 20901* (US).

**2. Ekmanochloa subaphylla** Hitchc., Man. Grasses W. Ind. 375. 1936. TYPE: Cuba. Oriente: Sierra de Nipe, Loma Picote, on overhanging limestone rocks, 500 m, 2 Nov. 1922, *E. L. Ekman 9870* (= *Amer. Gr. Nat. Herb. 1016*) (holotype, US; isotype, US). Figure 4G–L.

Tufted perennial. Vegetative culms 50–100 cm long (the erect portion shorter), erect or geniculate at the base, unbranched, with 4–6 fully developed leaves per complement. Leaves with sheaths 0.7–2 cm long, shorter than the internodes, the margins overlapping, membranous, glabrous; ligule 0.2 mm long, laciniate at the apex; pseudopetioles 0.6–1 mm long, pale to brownish, short-pilose; blades apparently early deciduous, 10–35 mm long, 1–4 mm wide, cuneate at the base, obtuse to subacute at the apex, shortly pilose to glabrous, the margins scaberulous toward the base, otherwise smooth and glabrous. Flowering culms 33–60 cm tall, erect, usually exceeding the vegetative culms, unbranched, with 2–3 bladeless leaves; peduncle 20–30 cm long, filiform, glabrous. Female inflorescence 30–40 mm long, with 3–5 spikelets at a distance of 4–6 mm from each other; pedicels 7–12 mm long, smooth, glabrous. Female spikelets 6–6.6 mm long, 0.9 mm wide; glumes much shorter than the body of the floret, unequal, membranous, glabrous, with obtuse, truncate, or emarginate or denticulate apices; lower glume 1–2.1 mm long, the upper 2.1–4.2 mm long; internode between upper glume and floret ca. 0.5 mm long, pilose; floret as long as the spikelet, 0.6 mm wide, acute, scabrous, pale to brownish; lemma 5-nerved, with an awn 5–10 mm long; palea shorter than the lemma, greenish; lodicules 0.4 mm long. Male inflorescence 17–23 mm long, with 6–12 spikelets; pedicels ca. 0.4 mm long, smooth or scaberulous, glabrous. Male spikelets 1.7–2.3 mm long, 0.5 mm wide, ellipsoid, subacute, glabrous, greenish; lodicules 0.2 mm long, brownish; stamens 2, the anthers 1.2 mm long. Caryopsis not seen.

*Phenology.* Apparently flowering from October to November.

*Distribution.* Limestone cliffs in the Alto Songo region of Oriente, Cuba, at elevations up to 500 m; last collected in 1960 (L. Catasús Guerra, 17 May 1982 letter to T. R. Soderstrom).

*Additional material examined.* CUBA. **Oriente:** Sierra de Nipe, in limestone hills at Río Jimbambay, 13 Oct. 1919, *Ekman 9870** (same number as type collection, but different locality and date) (US).

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# FENOLOGIA Y ESTRUCTURA FLORAL DE *TRICHILIA HAVANENSIS* JACQ. (MELIACEAE)[1]

*Delhy Albert Puentes,*[2] *Jesús Hernandez de Armas,*[2] y *Antonio López Almirall*[2]

## Resumen

Se realizó un estudio de fenología y estructura floral a la especie *Trichilia havanensis*. Se comprobó la dioecia de esta especie, a pesar de tener los órganos femeninos y masculinos en la misma flor. Un individuo que se había comportado como masculino durante los tres primeros años de observaciones fenológicas, fructificó posteriormente.

## Abstract

A phenological study carried out over 5 years is presented and flower morphology of *Trichilia havanensis* is given. Dioecy was confirmed in this species, despite the fact that female and male organs occur in the same flowers. A tree that behaved as male during the first 3 years of our phenological observations has fruited since 1988.

La dioecia es un fenómeno que ha sido estudiado por diferentes autores tales como Darwin (1877), Lewis (1941), Horovitz (1954). Estudios recientes han demostrado la presencia de especies dioicas que aparentan ser hermafroditas por tenor los órganos femeninos y masculinos en la misma flor.

Armstrong & Drummond (1986) señalaron que las flores estaminales y pistilares pueden adquirir aspecto similar para producir estímulo tanto visual como olfatorio al polinizador, sugiriendo que las flores pistiladas son probablemente miméticas de las flores estaminadas, mecanismo que ha sido clasificado por Little (1983) como decepción alimentaria por automimetismo. Otras hipótesis tratan de explicar la dioecia a partir del hermafroditismo; por ejemplo las de Arroyo & Raven (1975) quienes expresaron que el paso clave en la evolución de la dioecia es la reducción de los órganos femeninos en las plantas hermafroditas; y la de Lewis (1941) quien demostró la esporádica distribución de las especies dioicas en comparación con las familias hermafroditas (que se encuentran en todas partes), por lo que deduce que las especies dioicas han evolucionado a partir de representantes hermafroditas.

Luz de Armas (1985) en su estudio de las flores de *Chamissoa altissima* var. *altissima* expuso que ese taxon atravieza una fase evolutiva en la formación de una especie dioica, existiendo cuatro tipos florales en la misma. Las especies de la familia Meliaceae han sido consideradas como hermafroditas por numerosos botánicos, tales como Britton & Wilson (1923), Harms (1940), León & Alain (1951), y otros, debido a que aparentemente sus flores poseen los dos sexos.

Sin embargo, Styles (1972), de acuerdo con sus observaciones realizadas en el Suroeste y Centro de Africa, señaló que la mayoría de las especies de esta familia poseían flores unisexuales pero con rudimentos bien desarrollados del sexo no funcional. Años más tarde, este mismo autor resume el conocimiento adquirido hasta ese momento en cuanto a la biología floral de Meliaceae, lo cual fue utilizado por Pennington & Styles (1975, 1981) en el tratamiento taxonómico de la familia.

Nuestro trabajo tiene como objetivo dar a conocer los patrones de floración y fructificación de la especie *Trichilia havanensis* Jacq., perteneciente a la familia Meliaceae, en Cuba y ofrecer datos acerca de su estructura floral.

## Materiales y Metodos

Se realizaron observaciones fenológicas semanales durante cinco años (1985–1989) a 10 individuos de *Trichilia havanensis* localizados en el

[1] Queremos expresar nuestro agradecimiento al compañero Heriberto Rodriguez por la realización de los dibujos.
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Parque Metropolitano de La Habana. Este parque se encuentra situado a 23°6′N y a 82°26′O, presentando un suelo de rendzina negra (Obregón, com. pers.) y un bioclima termoxerochiménico con un periodo seco subhúmedo (Vilamajó et al., 1989). Los promedios mensuales de temperatura y las precipitaciones mensuales totales fueron tomadas del Instituto de Meteorología en la estación de Casa Blanca y con estos datos se confeccionaron los diagramas climáticos de Walter & Lieth (1960) (Fig. 1).

Las fenofases observadas fueron las siguientes:

Porcentaje de hojas
Botones (desde su aparición hasta la antesis)
Flores (desde el momento de la apertura hasta su desaparición)
Frutos (abarca todos los estadios de su desarrollo hasta la apertura)
Frutos abiertos (desde su apertura hasta que pierde las semillas)

Para la delimitación de las fenofases se empleó la metodología de Ramia (1981) y los datos fueron adaptados posteriormente a la escala de Fournier (1974) mediante el cual se establecen cinco rangos de aparición del caracter como sigue:

0 = ausencia del fenómeno observado
1 = presencia del fenómeno con una magnitud entre 1–25%
2 = presencia del fenómeno con una magnitud entre 26–50%
3 = presencia del fenómeno con una magnitud entre 51–75%
4 = presencia del fenómeno con una magnitud entre 76–100%

Para establecer los patrones de floración y fructificación de la especie, se compararon nuestros resultados con ejemplares localizados en los alrededores del Instituto de Ecología y Sistemática del Academia de Ciencias de Cuba, con observaciones de campo realizadas por nosotros en diferentes tipos de vegetación en la Provincia de Pinar del Río, y con 82 ejemplares de *T. havanensis* procedentes de diferentes localidades del país, ubicados en los herbarios de la Academia de Ciencias de Cuba (HAC) y Jardín Botánico Nacional (HAJB).

Para el estudio de la estructura floral, se tomaron 10 flores por cada árbol a las cuales se les midieron los siguientes indices:

A = longitud del tubo estaminal
B = longitud de la antera
C = longitud del ovario
D = ancho del ovario
E = longitud des estilo
F = longitud del estigma
G = longitud del pétalo
H = ancho del pétalo
I = longitud del disco nectarífero

TABLA 1. Relación de medias calculadas para las flores de *Trichilia havanensis*.

| Carácter | × general (mm) | × flores masculinas (mm) | × flores femeninas (mm) |
|---|---|---|---|
| A | 2.47 | 3.46 | 2.24 |
| B | 0.84 | 1.21 | 0.60 |
| C | 1.25 | 1.50 | 1.00 |
| D | 1.50 | 1.42 | 1.61 |
| E | 0.71 | 1.00 | 0.75 |
| F | 0.60 | 0.70 | 0.50 |
| G | 4.25 | 5.00 | 3.50 |
| H | 2.40 | 2.60 | 2.20 |
| I | 0.45 | 0.50 | 0.40 |

Con los datos obtenidos se confeccionaron los gráficos de Jentys-Szaferowa (1959). En este método se calculan previamente las medias aritméticas generales para cada carácter (de las plantas femeninas y masculinas tomadas como un todo) las cuales constituyen la linea unidad; posteriormente se grafican las diferencias de las medias de cada carácter con la media general (Tabla 1, Fig. 5).

Como caracteres cualitativos se observaron los tipos de apertura floral (completa o parcial) y la coloración de las anteras.

## RESULTADOS Y DISCUSION

Al analizar el porcentaje de hojas durante los cinco años observados, podemos ver que esta especie se comporta como siempreverde, ya que la pérdida en hojas no sobrepasa el 20% del total del follaje (Fig. 2).

La fenofase "botones" se ubica entre los meses de enero y marzo y "flores" a partir del mes de febrero, con un máximo en la segunda quincena de marzo, extendiendose hasta la primera semana de mayo (Fig. 2), de forma tal que puede catalogarse como una especie de floración tardía de acuerdo con la clasificación de Sarmiento & Monasterio (1983) y de floración corta según Ramirez & Brito (1987).

En los individuos más expuestos al sol se observó en todos los años mayor porcentaje de flores que en los que se encuentran en lugares mas sombreados.

En la Figura 3 están representados los promedios

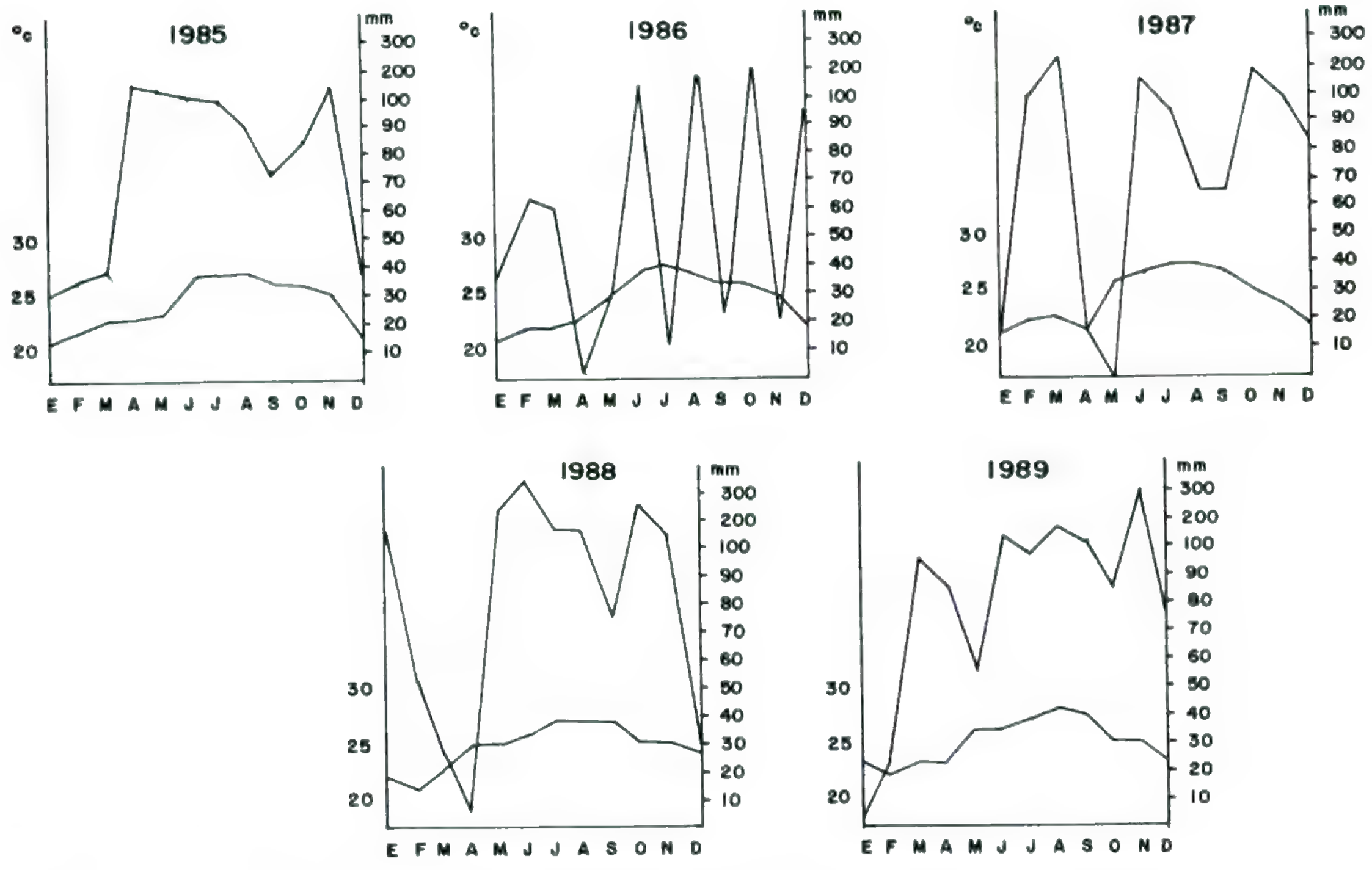


FIGURA 1. Diagramas climáticos del Parque Metropolitano de La Habana durante los años 1985–1989.

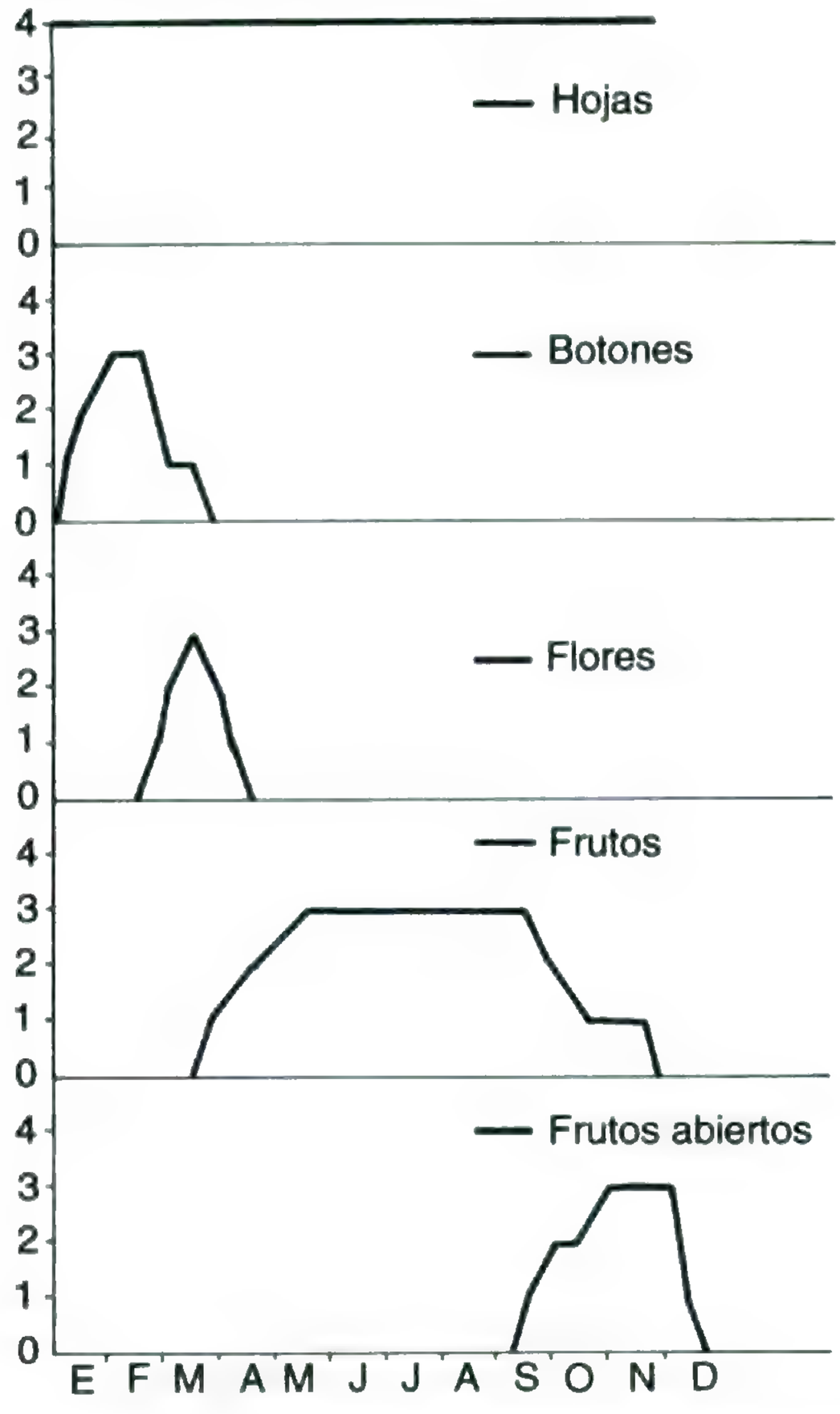


FIGURA 2. Promedios de cinco años de observaciones de las diferentes fenofases mediante el método de Fournier (1974).

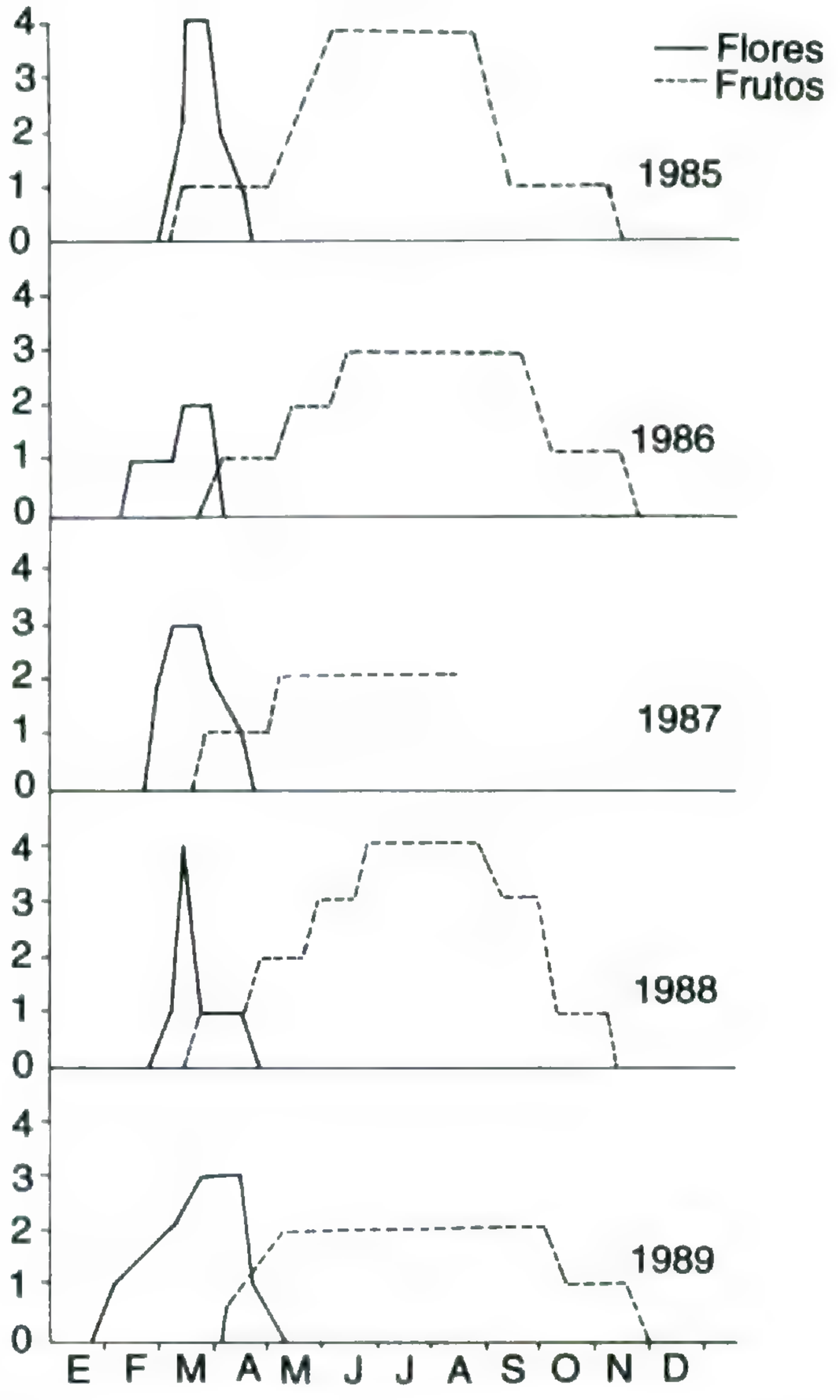


FIGURA 3. Promedios de producción anual de flores y frutos.

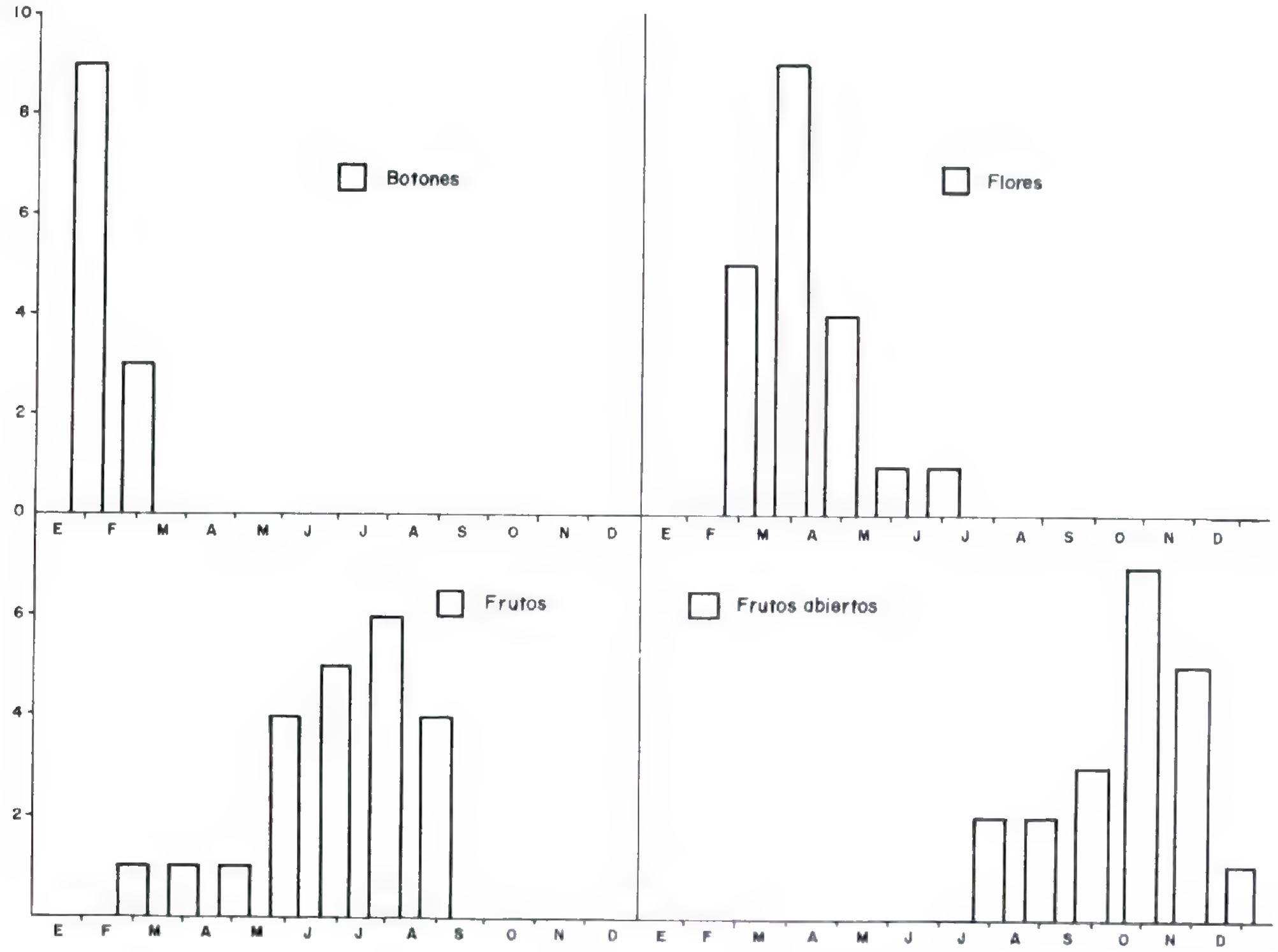


FIGURA 4. Histograma de frecuencias de los ejemplares de *Trichilia havanensis* depositados en los herbarios HAC y HAJB.

de producción anual de flores. Como podemos apreciar en los años 1985 y 1988 esta producción alcanza el rango 4 en la escala de Fournier lo que puede ser debido a un ligero aumento en las precipitaciones durante los años en cuestión ya que de acuerdo con Opler et al. (1976) y Mori & Prance (1987) la estacionalidad en los trópicos está fundamentalmente dada por este factor climático.

Los ejemplares florecidos procedentes de diferentes localidades del país ubicados en los herbarios anteriormente referidos (Fig. 4), los individuos situados en los alrededores del Instituto de Ecología y Sistemática, y las observaciones de campo realizadas en la provincia de Pinar del Río corroboran nuestros resultados, encontrándose los picos (máximos) de botones y flores en el mismo período que el encontrado como resultado de 5 años de observaciones fenológicas en el Parque Metropolitano de la Habana, lo que demuestra un gran sincronismo no solamente entre los árboles de una localidad, sino entre los individuos procedentes de las diferentes localidades del país.

Auspurger (1983) definió el sincronismo como un escape de las plantas a los depredadores de las flores y luego de las semillas, por lo que resulta una estrategia adaptativa para una exitosa polinización y dispersión de la semilla (Steven et al., 1987).

Con relación a los frutos, obtuvimos que durante los 5 años de observaciones, las plantas 3, 5 y 6 fructificaban y las restantes no, lo que concuerda con lo planteado con Pennington & Styles (1981) de que la especie *Trichilia havanensis* es dioica.

El período de fructificación de las plantas femeninas comienza generalmente desde mediados del mes de marzo hasta noviembre y abren sus cápsulas trimeras desde septiembre hasta finales de diciembre, etapa en la que si permanece algún fruto en la planta, este ya ha perdido las semillas, por lo que no se toman en consideración. De esta forma puede clasificarse como una especie de fructificación durante una temporada amplia según Castillo & Carabias (1982).

Como consecuencia de la abundante floración, la fructificación aparece con los mayores valores durante los años 1985 y 1988 (Fig. 3).

Los histogramas de frecuencias de "flores" y "frutos" confeccionados con los ejemplares depositados en los herbarios HAC y HAJB se encuentran ligeramente extendidos lo cual constituye una limitación de la fenología de herbario (Croat, 1969), pues los individuos pueden florecer en un año fuera de época, produciendo un alargamiento del período de la fenofase observada.

Las diferencias morfológicas entre las flores femeninas y masculinas se ponen de manifiesto en

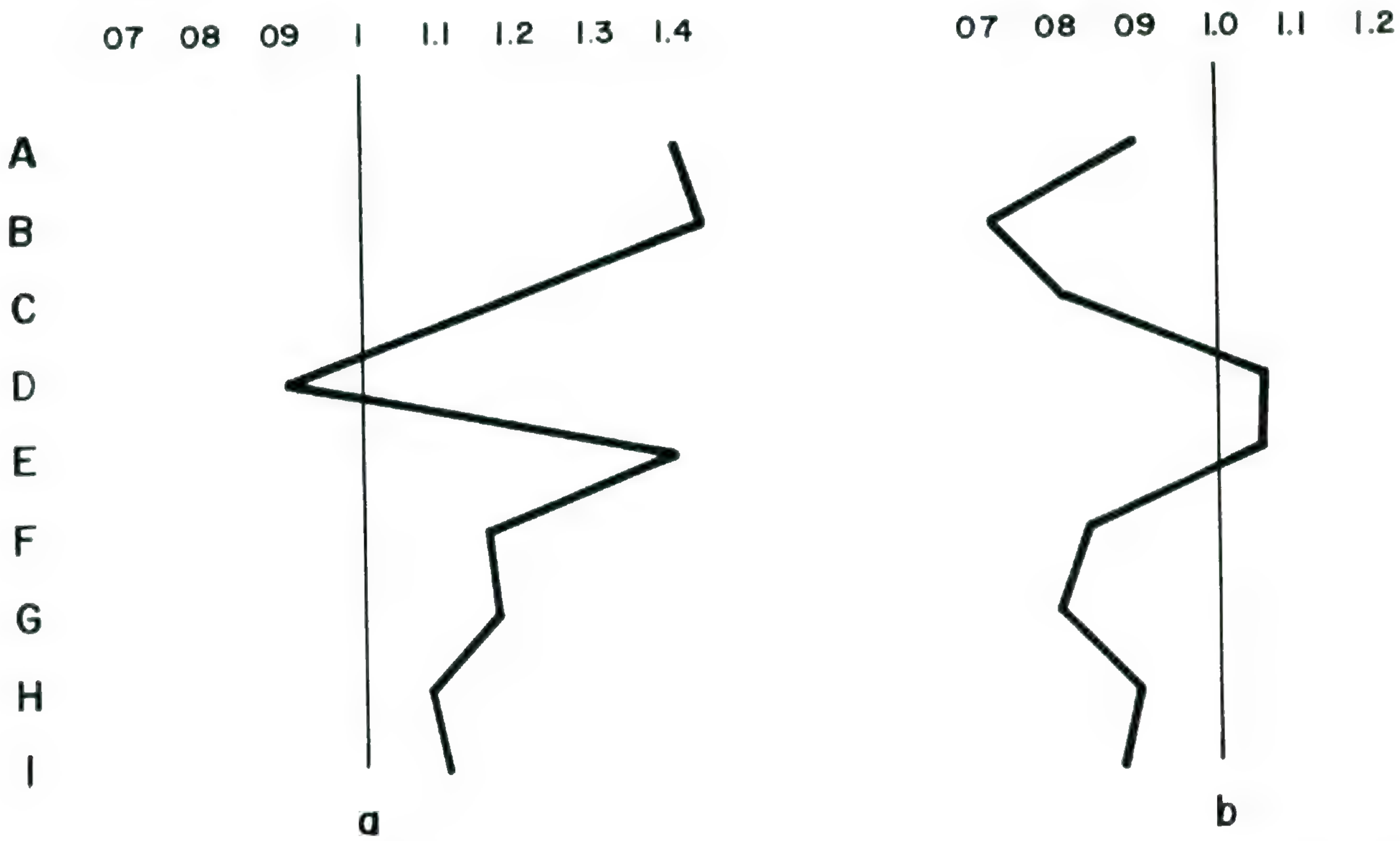


FIGURA 5. Gráficos de Jentys-Szaferowa medias calculadas en mm. —a. Ejemplares masculinos.—b. Ejemplares femeninos. Las letras corresponden con los caracteres y los números corresponden a las diferencias entre las medias particulares y la media general (ver materiales y métodos).

los gráficos de Jentys-Szaferowa (1959; ver Fig. 5, Tabla 1).

En las flores masculinas (Figs. 5a, 6A), todos los caracteres excepto el ancho del ovario (indice D) presentan mayores valores que en las femeninas (Figs. 5b, 6B).

Existen otras diferencias cualitativas entre las flores de ambos sexos como son las siguientes; la apertura floral en flores masculinas es completa, dejando descubierto totalmente al tubo estaminal y en las femeninas es parcial; y la coloración de las anteras en flores masculinas es amarilla mientras que en las femeninas es carmelita.

En período de floración encontramos una intensa actividad de la especie *Apis mellifera* L.

White en el prólogo de la monografía genérica de Meliaceae (Pennington & Styles, 1975), apuntó que un himenóptero insertaba su proboscis por una estrecha ranura formada entre las anteras y anteroides en *T. havanensis*, transfiriendo el polen de flores masculinas hacia la superficie estigmática de las flores femeninas.

Anteriormente Priestly y Scott, según de la Luz (1985), habían considerado que las flores de colores amarillo, blanco, y azul, con el color verde como follaje, eran visitadas con preferencia por los insectos, y atraen en especial a las abejas, las cuales a su vez prefieren las inflorescencias del tipo corimbo, capítulo y glomérulos, cuyas flores son reunidas y compactas, comportándose como superficies planas.

Este es el caso de las inflorescencias fasciculadas de *T. havanensis*, por lo que pensamos que la especie *Apis mellifera* L., abeja de miel, es probablemente la encargada de la polinización.

De acuerdo con lo señalado anteriormente, y si tomamos en cuenta que *Apis mellifera* es introducida en nuestro país, podemos corroborar lo planteado por Gentry (1986) de que la micrantia con flores agrupadas es poco específica para la polinización, motivo por el cual, muchas especies han podido establecerse en Cuba sin necesidad del agente polinizador.

Las hormigas son otros himenópteros que visitan las flores de *T. havanensis* pero estas no son consideradas como polinizadores, sino que se aprovechan y toman el néctar sin aportar beneficio a las plantas (Guerrant, 1981).

El que se hayan encontrado solamente tres plantas femeninas de las 10 estudiadas, está en correspondencia con lo que ocurre en la naturaleza de forma espontánea dentro de la familia Meliaceae, ya que el número de plantas masculinas es mucho mayor que el de femeninas (Styles, 1972).

Debemos señalar que la planta # 1, aunque se comportó durante tres años como masculina, en

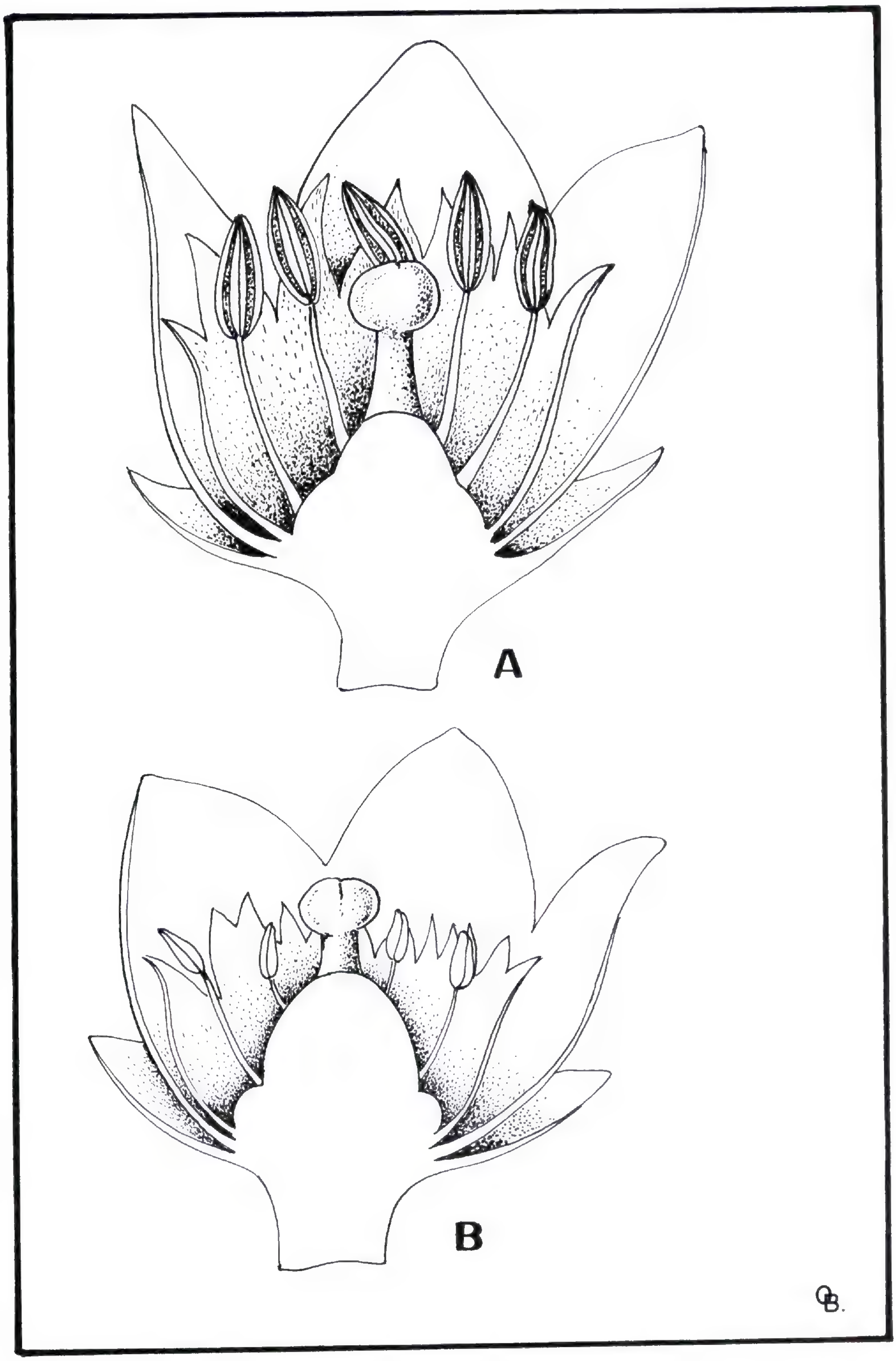


FIGURA 6. Flores de *Trichilia havanensis*—A. Flor masculina. B.—Flor femenina.

1988 comenzó a fructificar, desasrrollando frutos normales (hasta el rango 2 de la escala de Fournier).

A pesar de que fenómenos como el anteriormente expuesto han sido poco estudiados, existen algunos artículos referentes a la especie *Carica papaya* L. en los cuales se expone que aunque el tipo sexual básico está determinado genotípicamente, ciertos árboles machos y hermafroditas sufren reversiones sexuales de varios grados, atribuyéndole diferentes causas al mismo.

Por ejemplo, Muñoz Morales (1983), consideró que estas reversiones tienen dos origenes: ambiental y hereditario, y que los últimos producen cambios totales o parciales en las flores y órganos esenciales.

Este autor opina que las plantas femeninas no muestran variaciones por lo que son consideradas como el tipo floral de mayor estabilidad.

Ghosh & Sen (1975) señalaron la influencia del contenido de nitrógeno a favor de las plantas femeninas, así como el efecto de los reguladores del crecimiento, los cuales pueden alterar el proceso de floración provocando efectos de reversión sexual.

En nuestro caso, aunque no podemos descartar la influencia de los factores climáticos en este fenómeno, la situación en que se encuentran esas plantas es de "stress" ya que el bosque ha sido talado, ha aumentado el contenido de cal en el ambiente a causa de las construcciones que allí se producen, ha habido fuego (varias plantas del lugar han sido quemadas), o sea, que debido a la afectación antrópica observada en las áreas de estudio, los hábitos de vida de estos individuos han sido profundamente modificados.

De esta forma se demuestra que al igual que *Carica papaya* L., *Trichilia havanensis* es capaz de revertir sus hábitos reproductivos en condiciones extremas, lo cual probablemente es un mecanismo para la perpetuación de la especie.

## Conclusiones

Se pone de manifiesto la dioecia en la especie *T. havanensis* en Cuba, encontrándose un gran sincronismo en la floración de esta especie entre los meses de enero y abril. Se detecta mediante las observaciones fenológicas, que los principales agentes polinizantes parecen ser los himenópteros del grupo de los Apidos, colectándose especificamente la abeja de miel (*Apis mellifera*).

Las principales diferencias sexuales en las flores las encontramos en los caracteres del verticilo estaminal, mayor longitud del tubo, y anteras desarrolladas de color amarillo en las flores masculinas y tubo estaminal más pequeño y anteras carmelitas y arrugadas en las flores femeninas.

Existen otros caracteres que diferencian a las flores de ambos sexos como son: mayores dimensiones de los pétalos, disco nectarifero más desarrollado y apertura floral completa en flores masculinas, ocurriendo lo contrario en las femeninas.

Los fuertes cambios ecológicos observados en el hábitat de *Trichilia havanensis*, hacen que, al igual que ocurre con *Carica papaya* revierta sus hábitos reproductivos en condiciones extremas.

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# THE GENUS *CLERODENDRUM* (VERBENACEAE) IN MESOAMERICA[1]

*Ricardo M. Rueda*[2]


## Abstract

*Clerodendrum* is the largest genus of Verbenaceae, with about 560 species and varieties. It is most abundant in Africa and Asia, with only 20 species native to the New World. In Mesoamerica, 15 species and one variety are known: five of these species are native, and the remainder are cultivated as ornamental plants; several are more or less naturalized. Three of the introduced species and one of the native ones are first records for the Mesoamerican region.

## Resumen

*Clerodendrum* es el género más grande de la familia Verbenaceae con cerca de 560 especies y variedades. La mayoría de estas especies ocurren en Africa y Asia; solamente 20 especies son nativas al Nuevo Mundo. En Mesoamérica se conocen 15 especies y una variedad: de éstas solamente 5 especies son nativas; el resto son cultivadas como ornamentales, y algunas son naturalizadas. Tres de las especies cultivadas y una de las nativas son nuevos reportes para Mesoamérica.


The genus *Clerodendrum*, comprised of small trees, shrubs, woody vines, and perennial herbs, is well known for its showy and attractive ornamental species. This genus, with about 560 taxa, is the largest in the Verbenaceae and is taxonomically complex. It is native to tropical and subtropical regions of both hemispheres, most abundant in the Old World, and poorly represented in the New World, where, however, it is frequently cultivated and often naturalized. The name *Clerodendrum* is formed from two Greek words, "kleros" (chance or destiny) and "dendron" (tree). The reason for the application of the name to the genus is obscure, but it may well come from the ancient belief that some species had healing properties, while others acted in exactly the opposite way.

Historically, the taxonomy of the genus *Clerodendrum* has been confused (see Munir, 1989). Much of this can be attributed to the wide use of ornamental species with different varieties. Many species seem to be closely related, with some hybridization reported. Some of the species are extremely variable, due to environmental factors and horticultural selection, which has led taxonomists to describe many taxa.

Because several species are found mostly in cultivation in Mesoamerica, they have been poorly collected. The large size of the leaves and inflorescences also led to a tendency to collect few leaves and partial inflorescences. Thus, few complete collections are available for study. In addition, Burman's (1737) spelling "*Clerodendron*" instead of the correct spelling "*Clerodendrum*" of Linnaeus (1753) is often found in the literature, thus causing confusion. This study is based on (1) an exhaustive examination of the types, (2) morphological characters, and (3) geographical information available.

[1] This study was completed as a partial fulfillment of the M.Sc. degree in biology at the University of Missouri, St. Louis. I am grateful to Alwyn Gentry and Victoria Sork for direction and critical revision of the manuscript. The collaboration of the staff of the Missouri Botanical Garden was particularly valuable. Financial support was provided by a Fulbright fellowship through the Latin American Scholarship Program of American Universities (LASPAU). The following institutions made their herbarium collections available: BR, CAS, CHAPA, CR, DUKE, E, ENCB, F, GH, IJ, K, L, MA, MEXU, MICH, MO, MSC, NY, P, TEFH, TEX, US. The illustrations were prepared by J. Myers.

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## Morphological Characteristics

### HABIT

A liana habit is uncommon in Verbenaceae but is found in *Petrea* and *Holmskioldia*, the latter cultivated in the Mesoamerican region.

### WOOD

The genus does not have commercial value as a source of timber, probably because of its small stature. Record & Hess (1941) studied five species from Mesoamerica and the Caribbean region. They reported the wood of *Clerodendrum* to be yellow or whitish with a medium luster, moderately heavy with a fine texture, and easy to work with. Wood parenchyma is scanty, paratracheal. Wood fibers are in part septate, the pits numerous and medium-sized. Most of these anatomical characteristics are shared with such other genera of the family as *Aegiphila* and *Callicarpa* (both Verbenaceae). However, *Aegiphila* has wood parenchyma vasicentric to aliform and confluent, and *Callicarpa* has wood pores much larger than *Clerodendrum*.

### LEAVES

The leaves are simple decussate-opposite, ternate, or apically clustered and variable in size. *Clerodendrum aculeatum* has leaves ranging 0.9–4 cm long × 0.3–1.4 cm wide; *C. paniculatum* 6–35 cm long × 6–30 cm wide. Other American Verbenaceae genera with decussate-opposite leaves are *Verbena*, *Petrea*, and *Duranta*; however, none of them have the tremendous variability in size displayed in *Clerodendrum*. Like *Clerodendrum*, most Mesoamerican Verbenaceae have simple leaves, except *Vitex*, which has palmately compound leaves. Leaf shape is also variable; lanceolate in *Clerodendrum wallichii*; elliptic in *C. aculeatum*; and ovate in *C. japonicum*.

### VENATION PATTERNS

Venation patterns are variable, although most species are brochidodromous, sometimes only well above the base. Other less frequent types are craspidodromous as in *C. bungei*, and eucamptodromous as in *C. aculeatum* and *C. costaricense*. The angle of divergence of secondary veins from the midvein is variable but in most leaves is acute (45°–60°). In almost all of the species the secondary veins are broadly ascending and strongly arcuate. The number of secondary veins can vary from 5 to 9 on each side of the midvein.

### PETIOLES

Leaves are petiolate. The variability in petiole length is remarkable, 0.1–0.7 cm in *C. pittieri* and 1–40 cm in *C. paniculatum*. In a few species petioles are decurrent. Almost all of the species present elevated leaf scars, these becoming spinescent in such species as *C. aculeatum*.

### INDUMENTUM

The genus varies from glabrous or glandular-pubescent to pubescent with simple hairs. Calyx, petiole, pedicel, leaf, and twig pubescence are usually of different densities within a species. Most genera in Verbenaceae have annulate nodes, but some species of *Clerodendrum* have a band of tomentose hairs on the nodes. Disk-shaped glands on the calyx and scales on leaves are also present in some species.

### INFLORESCENCES

The inflorescences are both axillary and terminal, sometimes on the same plant. The inflorescences may range from 1 to 39 cm long and 1 to 25 cm wide. These inflorescences may be cymes, panicles, or solitary flowers, determinate or centrifugal, the flowers crowded or sparsely arranged. These types of inflorescences are also present in other genera such as *Aegiphila* and *Callicarpa*, but the flowers in these genera are regular and the stamens equal, unlike *Clerodendrum*, which has irregular flowers and didynamous stamens. Almost all the species of *Clerodendrum* have foliaceous bracts and linear-lanceolate bracteoles.

### CALYX

The calyx varies in size, ranging from 2 to 18 mm long. It is gamosepalous, commonly green, less often red or white, almost always campanulate, rarely elliptic, truncate, 5-lobed, glabrous or variously pubescent, sometimes glandular or lepidote, often accrescent in fruit. The accrescent calyx in fruits does not become thick and indurate as in *Aegiphila*, nor reflexed and patelliform as in *Callicarpa*.

### COROLLA

The size of the corolla ranges from 6 to 40 mm long to 3 to 20 mm wide, sometimes larger in the species of the Old World. It is gamopetalous, hypocrateriform, and may be white, red, pink, or purple. The limb is 5-parted, spreading at anthesis, mostly subactinomorphic. The corolla is glabrous,

pubescent, or glandular-puberulent. The corolla tube is not markedly curved and more or less 2-lipped, as in *Vitex*.

### STAMENS

The four stamens are didynamous, inserted on the corolla tube more or less at the same level. They are long-exserted, alternate with the corolla lobes; the anthers are glabrous, ovate or oblong, opening by longitudinal slits. This general pattern is shared by the majority of genera in Verbenaceae.

### POLLEN

The pollen is spheroidal, with echinate processes on the tectum. Rao & Tian (1974) described the pollen grains of *Clerodendrum inerme* Gaertner as spheroidal, 3-zonocolpate, the surface spiniliferous, and interspinular areas reticulate. Verbenaceae, including *Clerodendrum*, have pollen grains that are binucleate or seldom trinucleate, and most commonly triaperturate (Cronquist, 1981).

### PISTIL

The pistil protrudes more or less the same length as the stamens. It consists of a 2-carpelled ovary and a terminal style that is elongate and forked apically. The ovary is superior, imperfectly 4-loculate, glabrous, each locule 1-ovulate, the ovules pendulous, laterally attached, and hemianatropous.

### FRUITS

The fruit is drupaceous, mostly subglobose or obovoid, glabrous, usually separating at maturity into 4 pyrenes. The exocarp is more or less fleshy, often black or stramineous when mature, and the endocarp bony or crustaceous. Fruits range from 5 to 14 mm long and 5 to 8 mm wide. The fruits are not very useful in separating species because they are remarkably similar.

### SEEDS

The seeds may be 4, as in most Verbenaceae, or (by abortion) sometimes only 1–3. They are mostly oblong, with little or no endosperm. Most other American Verbenaceae uniformly have 4 seeds.

## Distribution and Ecology

*Clerodendrum* is most abundant in Africa and Asia, although a few native species occur in the New World, many more being cultivated and naturalized. In the New World the native species of *Clerodendrum* range from the northern part of Mexico (Tamaulipas and Oaxaca), and the West Indies, south to Peru (Ayacucho), and northern Argentina (Misiones). *Clerodendrum* occurs in the Old World from northern Africa (Senegal and Egypt) southward through the remainder of Africa and Madagascar. It also occurs eastward to China and Japan, and southward to Ceylon and northern New Zealand. Most of the species are in the Old World, especially in Zaire (67 species, 10 endemic), Tanzania (60 species, 13 endemic), Madagascar (67 species, 14 endemic), and the great Sunda Islands (66 species, 14 endemic) (Moldenke, 1980). The number of species in the New World is about 20, with most native species located in Colombia (6 species, 1 endemic), and Cuba (10 species, 7 endemic).

The species of *Clerodendrum* are reported growing in a wide variety of habitats. *Clerodendrum ligustrinum* (Fig. 1) is reported along the bank of a creek in Belize (*Lundell 6962*, F); *C. costaricense* (Fig. 2) was collected in cloud forest in Costa Rica; *C. pittieri* (Fig. 3) is reported growing in a mangrove area in Costa Rica on soil with up to 64‰ salinity (Jiménez & Soto, 1985); and *C. speciosissimum* (Campeche, Mexico; *Calzada et al. 6724*, MEXU) is found on limestone formations. Other habitats from which *Clerodendrum* has been reported include sand dunes (*C. ligustrinum*, Chiapas, Mexico; *Breedlove & Thorne 20913*, MO) and cloud forest (*C. philippinum*, Nicaragua; *Williams et al. 24693*, F).

*Clerodendrum* has been reported in association with many other plants. *Clerodendrum bungei* and *C. philippinum* are reported growing with *Quercus* in Chiapas, Mexico (*Breedlove 6837*, CAS, and *37852*, MEXU).

Altitudinally, species of *Clerodendrum* are more widely distributed in lowlands than in mountains. Most of the Mesoamerican species can grow very near sea level. Consequently, collections of *Clerodendrum* from higher elevations become progressively less frequent. Some of the species that may reach well into the mountains include *C. bungei* (2,100 m, Chiapas, Mexico; *Breedlove 6055*, F) and *C. philippinum* (1,400 m, Matagalpa, Nicaragua). The scarcity of high altitude records might be due partly to a decline in both individuals and species at higher altitudes.

## Animal Interactions

### POLLINATION AND DISPERSAL

Pollination in *Clerodendrum* is mostly carried out by butterflies, moths, and bees, which extract the nectar from the base of the corolla tube. In

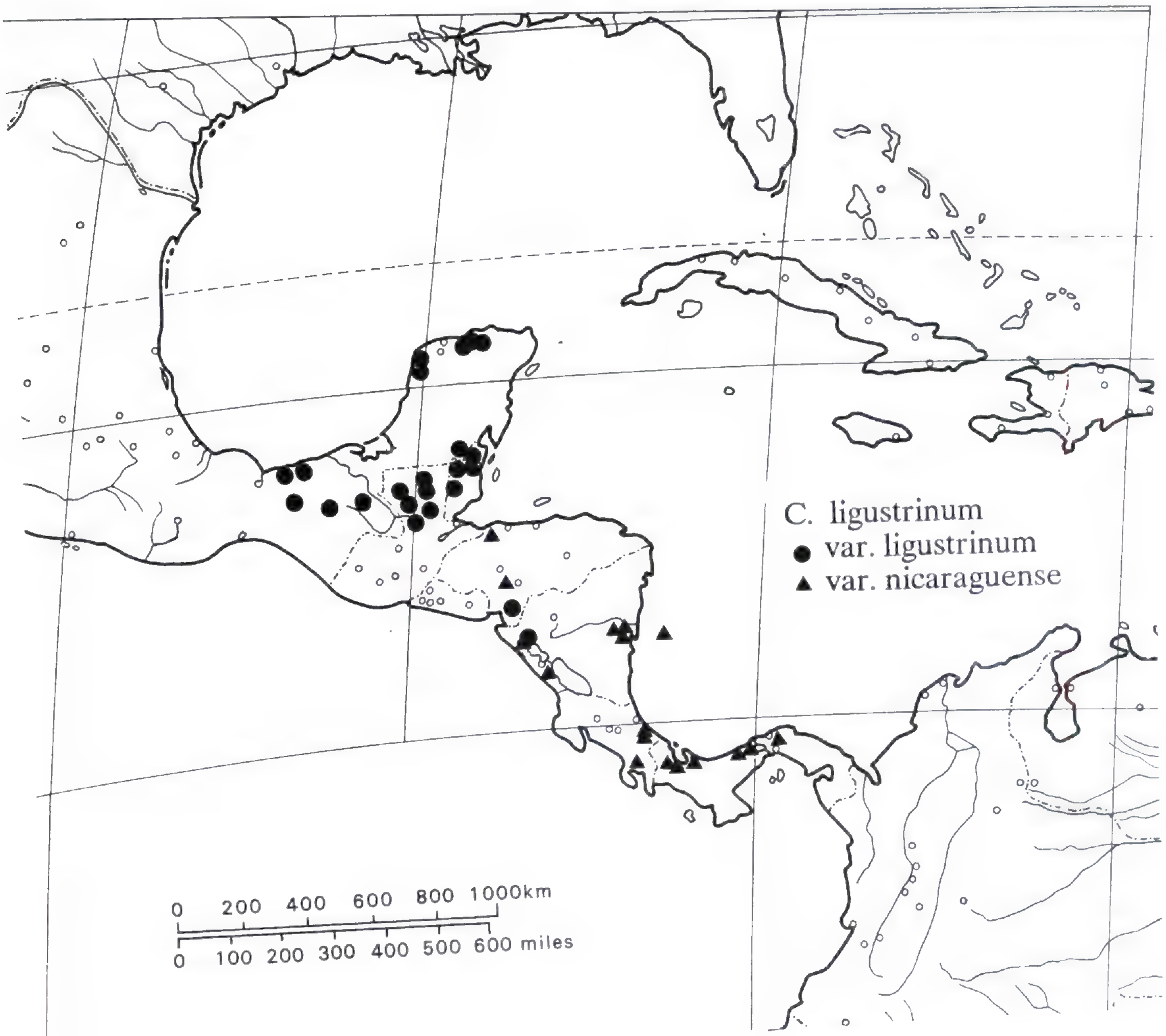


FIGURE 1. Distribution of *Clerodendrum ligustrinum* in Mesoamerica.

most species the stamens and style project from the lower side of the horizontally oriented flower; pollen is carried off on the underside of the insect. In such species as *C. aculeatum*, the flowers last more than one day, during which time the stamens first project and then curl back under the flower and leave the style exposed (Corner, 1952). In other species such as *C. serratum*, the stamens and style arch over the top of the flower and one of the petals is modified into a lower lip, which acts as a landing platform for visiting insects. In this last case the pollen is carried off on the upper side of the insect.

The fruits of *Clerodendrum* species are eaten by birds, which disperse the seeds (Moldenke, 1985). Ridley (1930) described the fruits of the genus as pulpy, often brightly colored, and distributed by birds. In many species the calyx provides a contrasting color, similar to those of red arils subtending black seeds. The pseudo-aril present in some species is actually a placental part of the pericarp that acts as an attractant to birds in the fruit dispersal process (van der Pijl, 1982).

ANTS

The relationship of some *Clerodendrum* species to ants was reported long ago. Beccari (1884) described *C. fistulosum* from Malaysia with internodes inhabited by *Camponotus* (*Colobopsis*) *clerodendri*. Mejía & Zanoni (*8508*, MO) reported many ants on plants of *C. speciosissimum* in the Dominican Republic. Dreisig (1988) reported the inflorescences of *C. speciosissimum* occupied by ants feeding on the nectar produced by the bracts. These ants belonged to three species, each having exclusive use of an inflorescence: *Wasmannia auropunctata* (Roger), *Camponotus abdominalis*

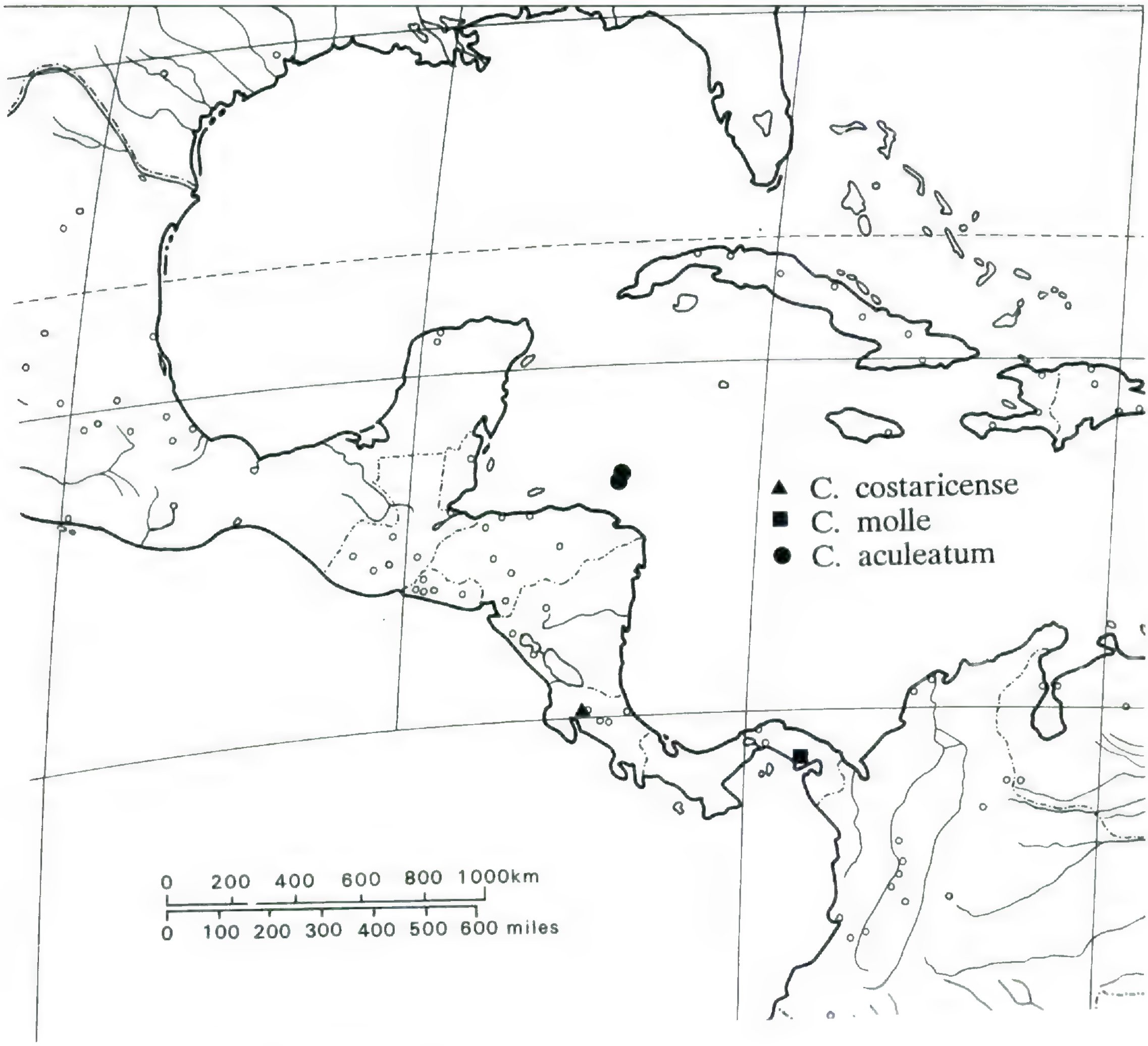


FIGURE 2. Distribution of *Clerodendrum costaricense*, *C. molle*, and *C. aculeatum* in Mesoamerica.

*floridanus* (Buckley), and *Conomyrma* sp. The foregoing observation, and especially the presence in some species of hollow stems and/or extrafloral nectaries (see Elias, 1983), clearly show that ants are intimately involved with some *Clerodendrum* species.

## CHROMOSOME NUMBERS

The chromosome numbers of the genus *Clerodendrum* are largely unknown. According to general chromosome indices (Cave, 1959, 1964; Bolkhovskikh et al., 1969; Moore, 1973; Kumar & Subramanian, 1987; Goldblatt, 1981, 1984, 1988), only 26 species and varieties have been studied to date, out of more than 560 species and varieties reported for the genus. Because *Clerodendrum* is mainly a paleotropical genus, most of the reports are from Old World taxa, among which are some of the species cultivated as ornamentals in Mesoamerica. Almost 50% of the species that are either cultivated or native in Mesoamerica have known chromosome numbers. Because of the poor cytological data on the genus there is not total agreement among researchers on the basic chromosome number. Thus, according to Moldenke (1985), the base chromosome number is $x = 12$ or 23; Raman & Kesavan (1963), $x = 15, 26$; and Mehra & Bawa (1969), $x = 12, 13$. It is at least clear that chromosome number in the genus is variable, ranging from $2n = 24$ in *C. aculeatum* to $2n = 184$ in *C. ugandense*.

## USES

The most popular use of *Clerodendrum* species worldwide is as ornamental plants. All of the Mesoamerican species except *C. costaricense* have

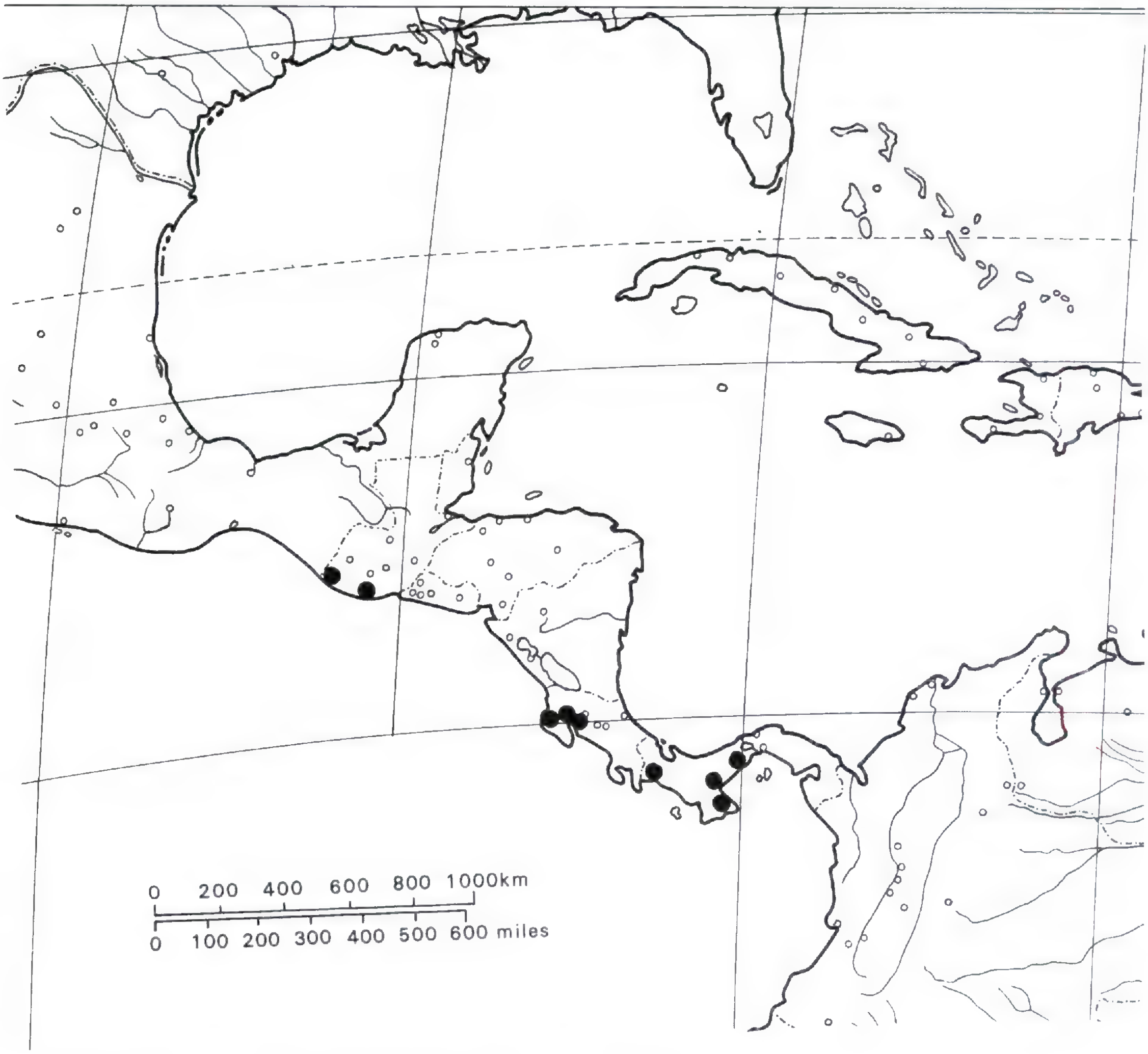


FIGURE 3. Distribution of *Clerodendrum pittieri* in Mesoamerica.

been planted ornamentally at one time or another. *Clerodendrum thomsonae* and *C. philippinum* are reported as ornamentals in Costa Rica (Pittier, 1978), and these two species plus *C. umbellatum* and *C. paniculatum* are cultivated as ornamentals in Nicaragua (pers. obs.). Molina (1975) listed seven species of ornamental *Clerodendrum* in Honduras; at least four species are cultivated as ornamentals in El Salvador (Standley & Calderón, 1941); and Gibson (1970) reported *C. philippinum* as one of the common ornamentals in Central America.

The folk use of the New World species of *Clerodendrum* is limited. In Yucatan, Mexico, the leaves of *C. ligustrinum* are used as a diuretic, even in the case of kidney stones (Mendieta & Del Amo, 1981). In Veracruz, Mexico, a leaf infusion is applied to snake-bites (Del Amo, 1979). In Petén, Guatemala, the leaves are also used in cooking to flavor fish (Gibson, 1970).

*Clerodendrum* is also important in having chemical compounds that may be used in medicine and industry. Gibbs (1974) reported that several species of *Clerodendrum* have D-manitol, saponins, tannins, cyanogenic (glycosides), quinones, and steroles.

## SYSTEMATIC TREATMENT

**Clerodendrum** L., Sp. Pl. ed. 1, 2: 637. 1753. TYPE; *Clerodendrum infortunatum* L. (Linn-810.1, microfiche, MO).

*Ovieda* L., Sp. Pl. ed. 1, 2: 637. 1753. TYPE: *Ovieda mitis* L. (Linn-807.1, microfiche, MO).

*Volkameria* L., Sp. Pl. ed. 1, 2: 637. 1753. TYPE: *Volkameria aculeata* L. (Linn-809.1, microfiche, MO).

*Volkmannia* Jacq., Pl. Hort. Schoenbr. 3: 48, pl. 338. 1798. TYPE: *Volkmannia japonica* Jacq. (type illustration ibid).

*Cornacchinia* Savi, Mem. Mat. Fis. Soc. Ital. Sci. Modena, Pt. Mem. Fis. 21: 184. pl. 7. 1837. TYPE: *Cornacchinia fragiformis* Savi (type illustration ibid).

Mostly shrubs, often scandent (arborescent in some species of the Old World), rarely herbaceous, unarmed, rarely the petiole base spinescent, glabrous or variously pubescent; branches usually tetragonal, sometimes medullose or hollow; nodes annulate sometimes with a band of hairs; leaf scars often prominent. Leaves simple, decussate-opposite or ternate, sometimes apically clustered, entire or variously dentate, sometimes lobed, mostly petiolate, glabrous or pubescent, often punctate beneath. Inflorescences cymose, cymes mostly loose-flowered (dense and capitate in some species of the Old World), pedunculate in the upper leaf axils, paniculate at the apex of the branches, often aggregate in terminal corymbs. Flowers actinomorphic or zygomorphic, often showy, perfect, hypogynous; calyx gamosepalous, green, sometimes the same color as the corolla, campanulate to tubular, sometimes inflated, the rim truncate to 5-toothed, often wide-spreading or accrescent with age; corolla gamopetalous, mostly hypocrateriform, usually purple, pink, red, or white, tube straight, sometimes incurved, limb 5-lobed, mostly subactinomorphic (plants bilabiate in some species of the Old World); stamens 4, didynamous, attached to the corolla tube, usually long-exserted; anthers glabrous, ovoid, 2-thecate, mostly basally attached, opening by longitudinal slits; pollen grains 3–6 colpate, tectum with echinate processes; ovary superior, 2-carpelled, imperfectly 4-locular, globose or oblong, glabrous, each locule 1-ovulate, ovules pendulous, laterally attached, hemianatropous; style terminal, filiform; stigma shortly bifurcate, sometimes globose. Fruit with calyx persistent, subtending or enclosing the fruit, sometimes colored; fruit drupaceous, often 4-sulcate, often brightly colored or black when mature, usually separating into 4 pyrenes or these sometimes united in pairs, by abortion sometimes 1–3 seeded; seeds oblong, endosperm absent; chromosome numbers: $x = 12$ or 23 (Darlington & Janaki, 1945; Darlington & Wylie, 1955; Hsu, 1968), $2n = 24–184$.

KEY TO SPECIES OF *CLERODENDRUM* IN MESOAMERICA

1a. Flowers pink, white, red, or purple, if white with the stigma globose; calyx always glabrous when flowers are pink; leaf scars never spinescent; plants cultivated, sometimes naturalized.
  2a. The largest leaves more than 15 cm long.
    3a. Inflorescences cymose, corymbose, 3–9 cm long.
      4a. Calyx 3 5 mm long; corolla tube 1.5–2.5 cm long (Fig. 4A) ..... 1. *C. bungei*
      4b. Calyx 1–1.5 cm long; corolla tube 1–1.5 cm long (Fig. 4B) ..... 2. *C. philippinum*
    3b. Inflorescences paniculate, 8–40 cm long.
      5a. Leaves not lobed.
        6a. Leaves glabrous.
          7a. Margins of leaves crenate, appressed teeth lacking; calyx 3–4 mm long ..... 3. *C. intermedium*
          7b. Leaves margin serrate with appressed teeth; calyx 8–16 mm long ..... 4. *C. japonicum*
        6b. Leaves pubescent ..... 5. *C. speciosissimum*
      5b. Leaves 3-lobed ..... 6. *C. paniculatum*
  2b. The largest leaves less than 15 cm long.
    8a. Corolla white to greenish white.
      9a. Corolla tube ca. 1.5 cm long; petioles 0.3–1 cm long ..... 7. *C. wallichii*
      9b. Corolla tube ca. 9 mm long; petioles 1–2.5 cm long ..... 8. *C. glabrum*
    8b. Corolla dark red to pink.
      10a. Calyx globose, 15 20 mm long, calyx lobes 1–1.8 cm long (Fig. 4C) ..... 9. *C. thomsonae*
      10b. Calyx campanulate, not globose, 7 13 mm long, calyx lobes 5–10 mm long (Fig. 4D) ..... 10. *C. umbellatum*

1b. Flowers pink, white, or yellowish, if white with the stigma bifid, not capitate; calyx pubescent, if glabrous with the leaf scars spinescent and flowers pink; plants native.
  11a. The largest leaves more than 4.5 cm long; leaf scars elevated but not spinescent.
    12a. Calyx glabrous; corolla tube ca. 1.2 cm long.
      13a. Leaves more than 10 cm long; calyx ellipsoid ..... 11. *C. costaricense*
      13b. Leaves less than 10 cm long; calyx campanulate.
        14a. Leaves decussate-opposite, glabrous beneath ..... 12. *C. ligustrinum*
        14b. Leaves ternate, pubescent beneath ..... 12a. *C. ligustrinum* var. *nicaraguense*
    12b. Calyx pubescent; corolla tube 1.8–2.5 cm long ..... 13. *C. molle*
  11b. The largest leaves less than 4.5 cm long; leaf scars spinescent.
    15a. Leaf scars spine-tipped; calyx lobed, pubescent; fruit subspheric ..... 14. *C. aculeatum*
    15b. Leaf scars not spine-tipped; calyx truncate, glabrous; fruit obovate ..... 15. *C. pittieri*

FIGURE 4. Inflorescence of:—A. *Clerodendrum bungei* Steudel (*Maxwell 94*);—B. *C. philippinum* Schauer (*Frye & Frye 2647*);—C. *C. thomsonae* Balf. f. (*Calderón 622*);—D. *C. umbellatum* Poiret (*Molina 10350*).

**1. Clerodendrum bungei** Steudel, Nomencl. Bot. ed. 2, 1: 382. 1840. *Clerodendrum foetidum* Bunge, Enum. Pl. China Bor. 52. 1833, non D. Don, 1825. TYPE: China, *Bunge 296* (holotype, LE not seen).

Shrub to 3 m tall; branchlets medullose, subterete or tetragonal, puberulent, lenticellate; leaf scars elevated. Leaves decussate-opposite, with an unpleasant odor when crushed; blade deltate-ovate or elliptic, 5–20 cm long, 3.5–15 cm wide, base truncate or acute, often decurrent, apex acute or acuminate, margin coarsely dentate, teeth often apiculate, puberulent, punctate beneath, often with glandular hairs on both surfaces, usually with discoid glands near the base beneath; midrib puberulent, secondaries 3–5 pairs; petioles 2–14.5 cm long, glabrous. Inflorescences cymose, terminal, rarely supra-axillary, subcapitate, corymbose 4–9 cm long, 3–12 cm wide, many-flowered, showy, puberulent; peduncles, 0–5 cm long; pedicels 1–6 mm long. Flowers usually fragrant; calyx tubular or campanulate, 3–5 mm long, outside glabrous and punctate, sometimes with a few disk-shaped glands, 5-lobed, lobes ovate, 1–3 mm long, acute or acuminate; corolla hypocrateriform or infundibular, usually red or rose to rose-purple, glabrous, 1.5–2.5 cm long, ca. 5 times as long as the calyx, limb 5-lobed, 1–1.5 cm wide, lobes oblong-ovate, 4–7 mm long; stamens 4, filaments long-exserted, to ca. 8 mm beyond the throat of the corolla tube, 1.2–1.4 cm long; ovary globose, style 2.8–3 cm long, exserted, shorter than or equal to the stamens. Fruit not seen; chromosome number: $2n = 108$ (Bolkhovskikh et al., 1969).

*Distribution and habitat.* This species occurs in Asia from China to northern India; it is cultivated worldwide and naturalized in tropical and subtropical regions. In Mesoamerica it has been collected in Mexico and El Salvador. *Clerodendrum bungei* is found on clay, limestone, or rocky soil, moist pastures, or frequently on oak-covered slopes, at altitudes up to 2,500 m.

*Vernacular names and uses.* "Bocamelia," "hortensia." The most important use is as an ornamental plant. The whole plant is decocted for lung weakness and cough (Duke & Ayensu, 1985).

*Note. Clerodendrum bungei* is frequently misidentified as *C. philippinum*. These two species can be separated using the length of the corolla in relation to the calyx. The corolla tube in *C. philippinum* only slightly exceeds the calyx in length, whereas the corolla tube in *C. bungei* is several times longer than the calyx. The holotype of *C. bungei* is probably deposited in LE. Although de Candolle (1880) and Sayre (1975) stated that the type may be in P, S. Barrier informed me that it is not in Paris.

*Selected specimens examined.* MEXICO. CHIAPAS: N end of San Cristóbal de las Casas, 2,100 m, 6 July 1964, *Breedlove 6055* (ENCB, F); W of Tenejapa center along the trail to Paraíso, 2,100 m, 4 Aug. 1964, *Breedlove 6837* (CAS, ENCB, MICH); along Mexican highway 190, 20 mi. NW of Comitán de Domínguez, 2,000 m, 23 June 1965, *Breedlove 10440* (CAS, ENCB, F, MICH, TEX, US); La Esperanza, Escuintla, 14 July 1947, *Matuda 16708* (F, MEXU). PUEBLA: ca. 2 mi. N of Teziutlan off road 125, 1,600 m, 27 June 1965. EL SALVADOR. SAN SALVADOR: cultivated in gardens, 1922, *Calderón 731* (US).

**2. Clerodendrum philippinum** Schauer in DC., Prodr. 11: 667 (as "*Clerodendron*"). 1847. TYPE: Philippine Islands, *Cuming 1096* (lectotype, designated by Howard & Powell (1968), GH).

*Volkmannia japonica* Jacq., Pl. Hort. Schoenbr. 3: 48, pl. 338. 1798. TYPE ILLUSTRATION: Japan, ibid, pl. 338.

*Clerodendrum fragrans* var. *multiplex* Sweet, Hort. Brit., ed. 1, 322. 1826. TYPE ILLUSTRATION: Curtis, Bot. Mag, 43: pl. 1834. 1816.

*Clerodendrum fragrans* var. *pleniflora* Schauer in DC., Prodr. 11: 666. 1847. TYPE: Martinique, *collector unknown s.n.* (holotype, G-DC 1908. 11: 666. 30, microfiche, MO).

*Clerodendrum philippinum* var. *subfertile* Mold., Phytologia 25: 368. 1973. TYPE: Sumatra, *Boeea 8394* (holotype, MICH not seen).

Shrub to 2 m tall; mostly reproducing vegetatively; branches medullose, angulated, puberulent, lenticellate; leaf scars often elevated. Leaves decussate-opposite or apically clustered; blade broadly ovate, 6–29 cm long, 5–28 cm wide, base cordate to subtruncate, often subcuneate, apex acute, margins coarsely serrate or sometimes the teeth apiculate, lightly strigillose-pubescent on both surfaces, usually more densely so on the venation beneath, sometimes with discoid glands near the base beneath; midrib glabrous, secondaries 3–5 pairs; petioles 2–20 cm long, puberulent. Inflorescences cymose, terminal, corymbose, 3–6 cm long, 4–9 cm wide, densely puberulent; peduncle 0–2 cm long; pedicels 1–5 mm long; bracts and bracteoles foliaceous 1–3 cm long. Flowers fragrant, often sterile; calyx campanulate, 1–1.5 cm long, sometimes with white blotches at or near the margins, sparsely strigillose-puberulent, outside with scattered disk-shaped glands, 5-lobed, lobes lanceolate, 4–10 mm long; corolla often "doubled," hypocrateriform, white to pink, glabrous, tube ampliate, 1–1.5 cm long, limb 5-lobed, 2 cm wide,

stamens and pistils often all modified into supernumerary petals; chromosome number: $2n = 46$ or 52 (Kumar & Subramanian, 1987).

*Distribution and habitat.* The original range of *Clerodendrum philippinum* is obscure, but it is likely native to Southern China to southern tropical Asia. It is cultivated and naturalized in tropical and subtropical regions worldwide. In Mesoamerica it has been collected from Mexico to Panama. This species is found in pastures, roadside embankments, riverbanks, open hillsides, slopes with *Quercus* and *Pinus*, and in disturbed high forest, at altitudes up to 2,100 m.

*Vernacular names and uses.* "Bocamelia," "flor de concha," "jasmín de noche," "mil flores," "misteriosa olorosa," "spanish jasmine," "verbena," and "viuda alegre." This species is one of the most common ornamentals of Mesoamerican gardens.

*Note.* The nomenclature of this species has been very confused. In 1804 Ventenat described *Volkameria fragrans* (*Clerodendrum philippinum*); he stated that this species was cultivated at the gardens in Paris and known as *Clerodendrum fragrans* and *Volkameria japonica*. But *Volkameria japonica* could not be used as a basionym in *Clerodendrum* for the plants now treated under *C. philippinum* because the epithet *japonica* was already occupied (Thunberg, 1780). *Clerodendrum fragrans* was published by Ventenat in synonymy, and therefore it is not a validly published name. *Clerodendrum fragrans* Willd., was illegitimate as published by Willdenow (1809) because he did not use Jacquin's type (Dan Nicolson, pers. comm.). To solve this problem, Howard & Powell (1968) designated the earliest valid name, *Clerodendrum philippinum* Schauer (1847).

*Selected specimens examined.* MEXICO. CHIAPAS: 8 km E of Las Margaritas, 1,700 m, 15 Sep. 1974, *Breedlove 37852* (MEXU). Hidalgo: Santa Ana, on Pan American Highway, 24 May 1939, *Frye & Frye 2647* (MO). BELIZE. EL CAYO: without precise locality, Mar.–June 1933, *Chanek 121* (F). GUATEMALA. BAJA VERAPAZ: El Niño Perdido, W of km 150/151, Aug. 1975, *Lundell & Contreras 19742* (F, MO). EL SALVADOR. SAN SALVADOR: vicinity of San Marcos, 5 Apr. 1922, *Standley 22796* (US). HONDURAS. CHOLUTECA: vicinity of San Marcos de Colon, 960–1,150 m, 12–22 Jan. 1949, *Standley 15796* (F). NICARAGUA. MATAGALPA: road to Senatorio de Aranjuéz, 1,000–1,400 m, 21 Feb. 1980, *Araquistain & Sandino 1401A* (MO). COSTA RICA. CARTAGO: Turrialba, 25 Aug. 1966, *Moldenke 1325* (TEX). PANAMA. BOCAS DEL TORO: vicinity of Almirante Bay, 19 Dec. 1938, *Von Wedel 15* (MO).

**3. Clerodendrum intermedium** Cham., Linnaea 7: "150" (i.e., 105). 1832. TYPE: Philippine Islands, *Cuming 481* (lectotype, here designated, L).

Shrub to 2 m tall; branches and branchlets tetragonal or subterete, medullose, puberulent, lenticellate; nodes annulate, the lower ones marked with a band of hairs; leaf scars slightly elevated. Leaves decussate-opposite; blades broadly ovate, 7–22 cm long, 6–20 cm wide, base deeply cordate, apex abruptly acute or acuminate, margin crenate, often abundantly light-dotted above and densely squamulose beneath; midrib puberulent, secondaries 5–7 pairs, the 2–4 lowest issuing palmately from the leaf base; petioles 2.5–23 cm long, lenticellate, strigillose. Inflorescence paniculate, terminal, 12–20 cm long, 8–18 cm wide, composed of 5–8 pairs of lax divaricate cymes, many-flowered; peduncles variable in length; pedicels 1–13 mm long, glabrous; bracts foliaceous, oblong-elliptic, the bracteoles and prophylls lanceolate to broadly linear, strigillose. Flowers with calyx campanulate, 3–4 mm long, granular lepidote, 5-lobed, lobes triangular-acuminate 2–3 mm long, equal to or longer than the tube; corolla hypocrateriform, bright red, outside puberulent and glandular, tube ca. 1.5 cm long, limb 5-lobed, ca. 1.3 cm wide, lobes oblong-ovate, 3–6 mm long, apically rounded-obtuse; stamens 4, long-exserted; filaments long-exserted ca. 2 cm beyond the throat of the corolla tube, 2.1–2.2 cm long; ovary oblong, style 2.3–2.5 cm long, exserted beyond the stamens. Fruit drupaceous, subtended by the calyx, 4–6 mm long, splitting into 2-bilobed, 2-seeded pyrenes at maturity; seed curved.

*Distribution and habitat.* *Clerodendrum intermedium* is native to the area between Taiwan and the Celebes and Sumatra islands. It is cultivated as an ornamental worldwide. In Mesoamerica it has only been collected in Honduras, which is the first report of this species in Mesoamerica.

*Vernacular names and uses.* In Honduras *Clerodendrum intermedium* is used as an ornamental plant. Gibbs (1974) reported the presence of cyanogens in the stem. Reis (1973) reported that the leaves of this species are made into a poultice and used for headaches.

*Note.* There are three species of *Clerodendrum* cultivated in Mesoamerica similar to *C. intermedium*. *Clerodendrum japonicum* has leaves similar to the leaves of *C. intermedium*, but the flowers are twice as big. *Clerodendrum intermedium* is also similar to *C. paniculatum* L. (not *C. paniculatum* Perrottet), but the latter has bigger inflorescences and lobulate leaves. The glabrate leaves of *C. intermedium* may be distinguished

easily from the pubescent leaves of the third species, *C. speciosissimum*. The type of this species is *Cuming 481*, as pointed out by Schauer (1847). He also commented that this material was deposited in B. This type seems to have been destroyed during the World War II, but there is one isotype in L, which is here designated as lectotype.

*Specimens examined.* HONDURAS. ATLANTIDA: Lancetilla valley, near Tela, 20–600 m, 6 Dec. 1927–20 Mar 1928, *Standley 56847* (F). MORAZAN: vicinity of El Zamorano, 800–850 m, 31 Aug. 1949, *Standley 23294* (F); El Zamorano, 800 m, 4 Oct. 1943, *Valerio 1092* (F).

**4. Clerodendrum japonicum** (Thunb.) Sweet, Hort. Brit., ed. 1, 322. 1826. *Volkameria japonica* Thunb., Nova Acta Regiae Soc. Sci. Upsal. 3: 208. 1780. TYPE: Japan, *Thunberg s.n.* (lectotype, here designated, UPS-14579, microfiche, MO).

*Clerodendrum coccineum* H. J. Lam, Verb. Malay. Archip. 296. 1919. TYPE: Java, *Buijsman 74* (holotype, BO not seen).

Shrub to 3 m tall; branches and branchlets tetragonal or subterete, medullose; puberulent, lenticellate; nodes annulate, the lower ones with a band of hairs. Leaves decussate-opposite; blades ovate, 10–30 cm long, 10–25 cm wide, base deeply cordate or auriculate, apex acute or acuminate, margin glandular serrate with appressed teeth, often light-dotted, puberulent on the venation and lipidote-squamulose beneath; midrib puberulent, secondaries 5–8 pairs, the 2–4 lower pairs issuing palmately from the leaf base, upper pairs ascending; petioles 2–15 cm long. Inflorescences paniculate, supra-axillary and terminal, 15–35 cm long, 13–30 cm wide; axillary peduncles 2–10 cm long; cymes 10–20 cm long, 4–10 cm wide, solitary in uppermost leaf axils; terminal panicles with 4–6 pairs of cymes; main peduncles 4–10 cm long, puberulent; pedicels 5–20 mm long; bracts foliaceous, a pair subtending each pair of cymes in the terminal panicles. Flowers with calyx campanulate, 8–16 mm long, puberulent, 5-lobed, lobes triangular-lanceolate, 10–14 mm long, apically acuminate; corolla hypocrateriform, deep red or scarlet, outside puberulent, tube curved, ca. 2 cm long, the limb 5-lobed, ca. 2.5 cm wide, lobes elliptic or oblong, 8–12 mm long; stamens 4, filaments long-exserted, ca. 3.5 cm beyond the throat of the corolla tube, 5–5.3 cm long; ovary oblong, style 6–7 cm long, exserted, shorter or equal to the stamens. Fruit not seen.

*Distribution and habitat.* *Clerodendrum japonicum* is native to Nepal, China, and upper Burma. It is also cultivated in tropical and subtropical regions and naturalized in Japan, Brazil, and Mexico. In Mexico this species is found in secondary deciduous forest, in secondary middle-elevation forest on rocky soil, and in coffee fields, at altitudes up to 1,300 m.

*Vernacular names and uses.* Floral bracts are chewed for hematuria and as a poultice for painful arthritis (Duke & Ayensu, 1985). In Mexico it is grown as an ornamental.

*Note.* There are three species of *Clerodendrum* cultivated in Mesoamerica that are similar to *C. japonicum* (see note under *C. intermedium*). The type material of *Clerodendrum japonicum* is deposited in UPS-Thunb. under the numbers 14579 and 14580. According to Roland Moberg, both numbers probably come from the same material divided into two sheets. However, neither of the two was designated as the holotype. The best specimen, 14579, should be regarded as the lectotype and 14580 as an isolectotype.

*Specimens examined.* MEXICO. OAXACA: Tuxtepec, 20 Apr. 1923, *Reko 4626* (US). VERACRUZ: 1 km E of Tenejapa, Hautusco–Cosmatepec road, 1,300 m, 2 Aug. 1979, *Avendaño & Calzada 445* (F); Tenochitlán, Colorado, Misantla–Tenochitlán road, 920 m, 27 Apr. 1976, *Hernández 175* (F, MO); Coetzala, by the road to Coetzapotitlán, 650 m, 25 Apr. 1976, *Vázquez 398* (F); Coetzala, by the road to Coetzapotitlán, 680 m, 25 Apr. 1976, *Velázquez 229* (F, MO).

**5. Clerodendrum speciosissimum** Morren, Hort. Belge 3: 322, pl. 68 (as "*Clerodendron*"). 1836. TYPE ILLUSTRATION: "Des Indes," cultivated by Baron Taffin at Van Geert Garden, Ghent, Belgium, pl. 68, ibid.

*Clerodendrum pulchrum* Fawcett in H. O. Forbes, Nat. Wand. East. Arch. 514. 1885. TYPE: Malaysia, *Forbes 3604* (holotype, BM not seen).

Shrub to 3 m tall; branches and branchlets tetragonal, usually medullose or hollow, puberulent, lenticellate; nodes annulate, sometimes with a band of hairs; leaf scars slightly prominent. Leaves decussate-opposite, blades broadly ovate, 8–25 cm long, 6–20 cm wide, base cordate, apex acute or short-acuminate, margin entire or irregularly crenate, above pubescent with whitish multicellular hairs, beneath with cinerous multicellular hairs, often with scattered disk-shaped glands along the midrib and secondaries beneath; midrib glabrous, secondaries 5–7 pairs, the two lower pairs issuing palmately from the leaf base, upper pairs arcuately

ascending; petioles 1.2–20 cm long, puberulent. Inflorescences terminal, panicle 8–35 cm long, 6–15 cm wide, composed of 5–13 pairs of cymes, puberulent; peduncles 3–6 cm long; pedicels 5–9 mm long, puberulent; bracts foliaceous, bracteoles and prophylls linear-setaceous, 1–5 mm long, puberulent. Flowers with calyx campanulate, 5–9 mm long, granular, puberulent, deeply 5-lobed, lobes ovate, 2–4 mm long; corolla hypocrateriform, red or scarlet, outside glandular-puberulent, tube 2–3 cm long, limb 5-lobed, 2–3 cm wide, 1.3–1.8 cm long; stamens 4, filaments long-exserted, ca. 2.5 cm beyond the throat of the corolla tube, 2.6–3 cm long; ovary oblongoid, style 4.5–5.5 cm long, exserted, shorter or equal to the stamens. Fruit drupaceous, subtended by the cupuliform calyx, globose, 5–8 mm long and wide, bilobed, separating into 4 pyrenes at maturity; chromosome number: $2n = 48$ (Bolkhovskikh et al., 1969).

*Distribution and habitat.* *Clerodendrum speciosissimum* occurs from Indonesia to the Caroline Islands and southeast to Tahiti and the Marquesas Islands. It is cultivated in most warm regions of the world. In Mesoamerica it has been collected from Mexico to Honduras.

*Vernacular names and uses.* The main use of this species is as an ornamental.

*Note.* There are three other species of *Clerodendrum* cultivated in Mesoamerica that greatly resemble *C. speciosissimum* (see note under *C. intermedium*). According to Moldenke & Moldenke (1983), the holotype of *C. speciosissimum* is a Morren collection taken from material given to him by Baron Taffin from the Van Geert Garden at Ghent, Belgium. In the original description, "August 1835" is reported as the date that the plant flowered for the first time, but a specimen either was not made or is missing. The type specimen should be in BR (fide Moldenke & Moldenke, 1983). However, according to Paul Bamps, curator of this herbarium, there are no Morren collections in BR (pers. comm.). Fortunately, the colored illustration (Morren, 1836: pl. 68) accompanying the original description is good enough to establish the identity of the species and may be considered as the type.

*Specimens examined.* MEXICO. CAMPECHE: Tixmucuy, road Holpechen–Tyxmucuy, 50 m, 11 Oct. 1980, *Calzada et al. 6724* (MEXU). YUCATAN: precise locality and date unknown, *Gaumer 909* (F, MO). GUATEMALA. ESCUINTLA: El Baúl Garden, 350 m, 3 Mar. 1921, *Tonduz 30* (F, US). EL SALVADOR. SAN SALVADOR: precise locality and date unknown, *Calderón 2533* (F); precise locality and date unknown, *Calderón 2544* (F, NY). HONDURAS. CORTES: San Pedro Sula, 80 m, 1951, *Pérez 12* (F).

**6. Clerodendrum paniculatum** L., Mant. Pl. 1: 90. 1767. TYPE: India, *collector unknown* (holotype, Linn 810.5, microfiche, MO).

*Clerodendrum splendidum* Wallich in Griffith, Not. Pl. Asiat. 4: 169. 1854. TYPE: India, *Wallich 1803* (holotype, K-Wall. 1803, microfiche, MO).

Shrub to 3 m tall; branches tetragonal, medullose or hollow, puberulent, lenticellate; nodes annulate, marked with a band of hairs; leaf scars slightly elevated. Leaves decussate-opposite; blades 3-lobed, ovate, 6–35 cm long, 6–30 cm wide, base deeply cordate and palmately veined, lobes apically acute to acuminate, central lobe larger and ovate, the others triangular, margin apiculate-denticulate to crenate-dentate or entire and with conspicuous glands mostly 3–10 mm apart, puberulent, often light-dotted above, densely squamose and punctate beneath; midrib puberulent, secondaries 5–7 pairs, the 2–4 lower pairs issuing palmately from the leaf base; petioles 1–40 cm long. Inflorescences terminal and sometimes axillary, terminal panicles 15–40 cm long and 13–35 cm wide; peduncles 2–10 cm long; pedicels 5–20 mm long. Flowers with calyx campanulate, 3–6 mm long, granular or puberulent, 5-lobed, lobes 2–4 mm long; corolla hypocrateriform, orange-red to scarlet, outside puberulent, tube 1–2 cm long, limb 5-lobed, ca. 1.2 cm wide, lobes oblong, 5–8 mm long; stamens 4, filaments long-exserted, ca. 2.2 cm beyond the throat of the corolla tube, 24–27 cm long; ovary oblong, style 3.5–4 cm long, exserted, shorter than the stamens. Fruit not seen.

*Distribution and habitat.* *Clerodendrum paniculatum* is native to the area from northern India eastward to Taiwan, south to Indonesia, and including the Andaman and Nicobar islands. It is cultivated in all warm regions of the world, where it is often naturalized. I have seen collections from Honduras, Nicaragua, Costa Rica, and Panama both from ornamentals and from plants naturalized into wet tropical forest, along streams, and in open grassy marshes at altitudes mostly below 500 m.

*Vernacular names and uses.* *Clerodendrum paniculatum* is used in Mesoamerica as an ornamental, especially cultivated along fencerows (Moldenke, 1973).

*Note.* There are three species of *Clerodendrum* cultivated in Mesoamerica that are similar to *C. paniculatum* (see note under *C. intermedium*). The holotype sheet (810.5) has the name Juan Bonge on it, but this may be a vernacular name. If this is the collector, it is an unknown one.

*Specimens examined.* HONDURAS. ATLANTIDA: Lancetilla Botanic Garden, 3 km SW from Tela, 10 m, 19 Apr. 1984, *Martínez 176* (TEFH). NICARAGUA. RIO SAN JUAN: San Juan del Norte, E side, 5 m, 2 Dec. 1982, *Araquistain 3371* (MO). COSTA RICA. HEREDIA: outskirts of Puerto Viejo or in the town itself, 13 July 1986, *Wilbur 39925* (DUKE). PANAMA. COLON: Barro Colorado Island, Canal Zone, in clearing at laboratory, 3 Dec. 1967, *Croat 4065* (MO).

**7. Clerodendrum wallichii** Merr., J. Arnold Arbor. 33: 220 (as "*Clerodendron*"). 1952. *Clerodendrum nutans* Wallich, Numer. List. 49, no. 1793. 1829. TYPE: Bangladesh, *Wallich 1793* (holotype, K; holotype and isotype on microfiche, MO), non W. Jack, 1820.

Shrub to 3 m tall; stems or branches usually simple and arching, medullose, tetragonal, puberulent; nodes annulate with a band of hairs; leaf scars slightly elevated. Leaves decussate-opposite or ternate; blades oblong-lanceolate, 4–13 cm long, 1–3 cm wide, basally acute or subcuneate, apex long-acuminate or caudate, margin entire or undulate, puberulent on both surfaces, punctate beneath; midrib glabrous, the secondaries 5–7 pairs; petioles 0.3–1 cm long, often slightly alate, puberulent. Inflorescences terminal, paniculate, puberulent, 9–30 cm long, 4–10 cm wide, with 6–10 pairs of divaricate cymes, each cyme 1–5-flowered; peduncles 1–4 cm long; pedicels 4–10 mm long; bracts foliaceous, subtending each pair of cymes. Flowers with calyx campanulate, slightly pentagonal, 0.5–1.2 cm long, puberulent, 5-lobed, lobes triangular-acuminate, 0.3–0.8 mm long; corolla hypocrateriform, white to greenish white, puberulent, tube ca. 1.5 cm long, limb 5-lobed, ca. 1.5 cm wide, lobes ovate, 0.9–1.3 cm long; stamens 4, filaments long-exserted, ca. 2.5 cm beyond the throat of the corolla tube, 2.3–2.8 cm long; ovary oblong, style 3–3.5 cm long, exserted, shorter than the stamens, stigma bifid, capitate. Fruit not seen.

*Distribution and habitat. Clerodendrum wallichii* is native to southern Asia, from the Himalayas to southern China, south to Indochina, the Nicobar Islands, and northeast to Pakistan. It is cultivated as an ornamental in all tropical and subtropical countries and in greenhouses elsewhere. In Mesoamerica it has been collected in Guatemala, El Salvador, and Costa Rica.

*Vernacular names and uses.* "Martinica" and "misteriosa." In Mesoamerica this species is only used as an ornamental.

*Note.* In Mesoamerica there are no other species similar to *Clerodendrum wallichii*. In addition, it is the only species of *Clerodendrum* known in Mesoamerica with a capitate-bifurcate stigma. The name *Clerodendrum nutans* was changed by Merrill in 1952 because this name had been used by Jack in 1820.

*Specimens examined.* GUATEMALA. ESCUINTLA: at S base of Volcán de Fuego, Finca Zapote, 780 m, 2 May 1939, *Standley 64521* (F). EL SALVADOR. SAN SALVADOR: vicinity of San Salvador, 650–850 m, 30 Mar.–24 Apr. 1922, *Standley 23645* (US). COSTA RICA. SAN JOSE: vicinity of San José, 1,130 m, 4 Dec.–10 Feb. 1926, *Standley 52498* (US).

**8. Clerodendrum glabrum** E. Meyer, Comm. Pl. Afr. Austr. 273 (as "*Clerodendron*"). 1838. TYPE: South Africa, *Drège s.n.* (holotype, G-DC 1906. 11: 661.2, microfiche, MO; isotype, MO).

*Ehretia triphylla* Hochst., Flora 27: 830. 1844. TYPE: South Africa, *Krauss 100* (isotype, MO).
*Clerodendrum ovale* Klotzsch in W. Peters, Naturw. Reise Mossambique 1: 257. 1861. TYPE: East Africa, *collector unknown s.n.* (holotype, B not seen).

Shrub to 3 m tall (sometimes a tree to 12 m tall in the Old World); branchlets solid, subterete or tetragonal, glabrous, lenticellate; leaf scars elevated. Leaves decussate-opposite or ternate with an unpleasant odor when crushed; blades elliptic-ovate to oblong, 3–8 cm long, 3–5 cm wide, base acute or short cuneate, apex acute or obtuse, margin entire, undulate, glabrous on both surfaces, densely punctate beneath; midrib puberulent, secondaries ca. 6 pairs, all ascending; petioles 1–2.5 cm long, lenticellate, glabrous. Inflorescences axillary in the uppermost axils and terminal, cymes opposite or whorled, many-flowered, puberulent, 7.5 cm long and 6 cm wide, several times bifurcate, terminal panicles corymbose; peduncles 1–3 cm long; pedicels 2–10 mm long, puberulent; bracts foliaceous, bracteoles and prophylls linear, 2–4 mm long. Flowers fragrant; calyx campanulate, 3–5 mm long, puberulent and glandular-lepidote, 5-lobed, lobes 1–3 mm long, shorter than the tube; corolla hypocrateriform, white, outside puberulent and glandular, tube ca. 9 mm long, limb 5-lobed, ca. 1 cm wide, lobes obovate, 3–4 mm long; stamens 4, filaments long-exserted, ca. 17 mm beyond the throat of the corolla tube, 2.5–2.7 cm long; ovary oblongoid, style 3–3.2 cm long, exserted, equal to or longer than the stamens. Fruit drupaceous, subtending calyx cupuliform, 5–9 mm long and wide, sulcate; seeds 1–2, oblong.

*Distribution and habitat. Clerodendrum glabrum* is native from Kenya to Angola and

throughout South Africa, and the Comoro and Seychelles islands. In Mesoamerica it has only been collected in Guatemala, which is the first report in Mesoamerica.

*Vernacular names and uses.* "Palo de perico." It is presumably an ornamental in Guatemala.

*Note.* The sole collection of *Clerodendrum glabrum* known from Mesoamerica seems to have been collected in an abandoned garden, since its accompanying label does not indicate that it was taken from a cultivated plant. The only similar species to *C. glabrum* in Mesoamerica is *C. ligustrinum*, from which it may be distinguished by the length of the calyx and corolla. The calyx and corolla of *C. ligustrinum* are twice as long as those of *C. glabrum*.

*Specimen examined.* GUATEMALA. GUATEMALA: San Juan Sacatepéquez, 1,480 m, *Morales 1874* (F, NY).

**9. Clerodendrum thomsonae** Balf. f., Edinburgh New Philos. J., ser. 2, 15: 233. pl. 2 (as "*Clerodendron*"). 1862. TYPE: from plant cultivated at the Edinburgh Botanical Garden sent by W. C. Thomson from Old Calabar, southern Nigeria, *collector unknown s.n.* (lectotype, here designated, E).

Shrub 2–2.5 m tall; branchlets tetragonal, medullose, puberulent, lenticellate; leaf scars often circular, corky, elevated. Leaves decussate-opposite; blades elliptic or elliptic-ovate, 4–13 cm long, 2–6 cm wide, base rounded or subacute, apex acuminate or short-acuminate, margin entire, ciliate, puberulent on both surfaces; midrib puberulent, secondaries 5–7 pairs, the lowest pair issuing palmately from the leaf base; petioles 0.5–3 cm long, puberulent. Inflorescences axillary, cymose, puberulent, 5–13 cm long, 5–15 cm wide, individual cymes 5–9 cm long, 4–8.5 cm wide, often trichotomous first and then dichotomous; peduncles 2–6 cm long, puberulent; bracteoles and prophylls linear, 2–11 mm long, puberulent. Flowers with calyx globose, coarse, ± pentagonal, 1.5–2 cm long, puberulent, 5-lobed, lobes ovate, 1–1.8 cm long, acuminate; corolla hypocrateriform, dark red to scarlet, externally glandular puberulent, internally puberulent, tube ca. 2.5 cm long, limb 5-lobed, ca. 1 cm wide, lobes oblong-elliptic, 5–9 mm long, obtuse or acute; stamens 4, filaments long-exserted, ca. 1.5 cm beyond the throat of the corolla tube, 2–2.2 cm long; ovary oblong, style filiform 2.9–3.2 cm long, exserted, shorter or equal to the stamens. Fruit drupaceous, covered by the calyx, 2.3 cm long, round or depressed-globose, 10–14 mm long and wide, glossy black, 2-bilobed; seeds oblong; chromosome number: $2n = 42$, 46, 48, or 50 (Bolkhovskikh et al., 1969).

*Distribution and habitat.* *Clerodendrum thomsonae* is a western African species that ranges from Senegal to Zaire. It has been collected throughout Mesoamerica.

*Vernacular names and uses.* "Arete de india," "arroz y frijoles," "bandera," "corazón sangrante," "fucsia," "lazo de amor," "matrimonios," "misteriosa," "moros y cristianos," "pasión de cristo," and "rice and beans." It is used in Mesoamerica exclusively as an ornamental.

*Note.* In Mesoamerica *Clerodendrum thomsonae* is not known to escape from cultivation. This species is very similar to *C. umbellatum*. However, the calyx in *C. thomsonae* is twice as large as in *C. umbellatum*. In addition, the calyx of *C. thomsonae* is coarser in texture than is that of *C. umbellatum*. The specimen in E, number 32/89 (1) was collected in January 1862, and the number 32/89 (2) was collected in July 1863. However, it is not known which is the holotype. Therefore, it is necessary to select a lectotype. The specimen 32/89 (1) should be regarded as a lectotype and 32/89 (2) as an isolectotype.

*Selected specimens examined.* MEXICO. CHIAPAS: Escuintla, 2 May 1948, *Matuda 17699* (F, MEXU). GUATEMALA. IZABAL: vicinity of Quirigua, 75–225 m, 15 31 May 1923, *Standley 24316* (GH, US). EL SALVADOR. SAN SALVADOR: vicinity of San Salvador, 650–850 m, 30 Mar. 24 Apr. 1922, *Standley 22377* (US); without specific locality, 1922, *Calderón 622* (MO). HONDURAS. COMAYAGUA: vicinity of Comayagua, 600 m, 12–23 Mar. 1947, *Standley & Chacón 5645* (F). NICARAGUA. ZELAYA: Bluefield, 29 Aug. 1948, *Long 208* (F). COSTA RICA. ALAJUELA: Ojo de Agua, 22 June 1946, *Echeverría 452* (CR). PANAMA. COLON: Canal Zone, 20–80 m, 13 Feb. 1911, *Pittier 2739* (US).

**10. Clerodendrum umbellatum** Poiret in Lam., Encycl. 5: 166. 1804. TYPE: West Africa, *Smeathman s.n.* (holotype, P-LA 6207. 510: I. 6, microfiche, MO; isotype, K).

*Clerodendrum hirsutum* G. Don, Edinburgh New Philos. J. 11:349. 1824. TYPE: West Africa, *Don s.n.* (holotype, BM not seen).

Shrub 0.2–3 m tall; branches and branchlets tetragonal, medullose or hollow, puberulent, sometimes lenticellate; leaf scars often elevated. Leaves decussate-opposite; blades ovate, elliptic or oblong, 4–13 cm long, 2–9 cm wide, base obtuse or subcordate, apex short-acuminate or acute, margin entire, impressed punctate beneath; midrib puberulent, secondaries 5–7 pairs, lower 1–2 pairs issuing palmately from the base; petioles 1–3 cm

long, puberulent. Inflorescences axillary, cymose, in a terminal panicle, 10–25 cm long, 12–24 cm wide, individual cymes several times branched, flowers 5–11 cm long, 3–12 cm wide, terminal panicles subumbellate; peduncles 2.5–6 cm long, puberulent; pedicels 5–15 mm long; bracts narrowly elliptic. Flowers fragrant; calyx campanulate, 0.7–1.3 cm long, puberulent, 5-lobed, lobes ovate or lanceolate, 0.5–1 cm long; corolla hypocrateriform, dark red to pink, with a pinkish or reddish throat, outside puberulent, tube ca. 2.2 cm long and ca. 1 cm wide, lobes obovate, 7–9 mm long; stamens 4, filaments long-exserted, ca. 2 cm beyond the throat of the corolla tube, 2.3–3 cm long; ovary oblong, style 3.8–4.2 cm long, exserted, equal to the stamens; chromosome number: $2n = 24$ or 48 (Goldblatt, 1981).

*Distribution and habitat.* *Clerodendrum umbellatum* is an African species that occurs from Senegal and Mali southeast to Kenya and Tanzania. In Mesoamerica this species has been collected in Mexico, Honduras, Nicaragua, and Panama; it may also be naturalized in the area. This is the first report of *C. umbellatum* in Mesoamerica.

*Vernacular names and uses.* *Clerodendrum umbellatum* is used as an ornamental, especially in fencerows.

*Note.* The label data indicate that this species sometimes escapes in Mesoamerica. An example is *Ramos 2* found growing in pine plantations in La Paz, Honduras.

*Selected specimens examined.* MEXICO. CHIAPAS: Huixtla, along the street of Huixtla, 30 m, 16 Jan. 1972, *Breedlove 23780* (CAS). TABASCO: Comalcalco, km 28 of the road Cardenas to Comalcalco, 25 Jan. 1979, *Cowan 1943* (TEX). HONDURAS. ATLANTIDA: La Lancetilla experimental station, 20 m, 17 Mar. 1962, *Molina 10350* (F, US). ISLAS DE LA BAHÍA: Isla de Guanaja, at sea level, 28 July 1984, *Nelson & Cruz 9032* (TEFH). LA PAZ: Sigamane, 5 km E of Marcala, 1,460 m, 26 June 1985, *Ramos* 2 (TEFH). NICARAGUA. MANAGUA: Península de Chiltepe, Comarca Alfonso González, 80–100 m, 3 July 1980, *Guzmán et al. 252* (MO). RIVAS: Isla de Ometepe, Balgue, 40–100 m, 18 Jan. 1987, *Moreno 19659* (MO). PANAMA. LOS SANTOS: Las Tablas, La Baja, 20 June 1971, *Carrasquilla 154* (F).

**11. Clerodendrum costaricense** Standley, Field Mus. Publ. Bot. 18: 1002 (as "*Clerodendron*"). 1938. TYPE: Costa Rica, *Smith H588* (holotype, F; isotype, MO; fragment and photo, NY).

Shrub to 5 m tall; branchlets and twigs medullose, subterete, lenticellate; leaf scars elevated. Leaves decussate-opposite; blades oblong-elliptic, 11–14 cm long, 6–9 cm wide, base obtuse, apex short-acuminate, margin entire, undulate and thickened, punctate beneath; midrib prominent, secondaries ca. 6 pairs; petioles 1–2 cm long, sparsely lenticellate. Inflorescences axillary, 3-flowered, glabrous; peduncles 3–6 cm long; pedicels 0.5–1 cm long, glabrate, bracts foliaceous, oblong-lanceolate, bracteoles linear-setaceous, 2–3 mm long, puberulent. Flowers with calyx ellipsoid, 10–12 mm long, glabrous, shortly lobed, lobes ovate, apically caudate-apiculate; corolla hypocrateriform, pale greenish yellow at anthesis, fading to brown, glabrous, the tube cylindric, ca. 1.2 cm long, the limb ca. 2 cm wide, the lobes spreading, oblong, as long as the tube, apically obtuse. Other floral parts not examined. Fruit unknown.

*Distribution and habitat.* *Clerodendrum costaricense* has only been collected in Alajuela, Costa Rica (Fig. 2). It was found in the Caribbean cloud forest climbing over vegetation at the edges of woodland, at 1,650 m.

*Vernacular names and uses.* None reported.

*Note.* The available material of this species is very poor, especially in reproductive structure. The specimens have only buds or incomplete flowers, and the description is accordingly incomplete.

*Specimen examined.* COSTA RICA. ALAJUELA: La Peña del Zarcero, 1,650 m, 4 Apr. 1938, *Smith H588* (F, MO, NY).

**12. Clerodendrum ligustrinum** (Jacq.) R. Br., in W. T. Aiton, Hortus Kew. ed. 2, 4: 64. 1812. *Volkameria ligustrina* Jacq., Coll. Suppl. 118, pl. 5, fig. 1. 1797. TYPE: material cultivated in Vienna, Austria, from "Mauritius island," plate 5, fig. 1, ibid.

*Clerodendrum culinare* Sessé & Mociño, Fl. Mexic., ed. 2, 2: 151. 1894. TYPE: Mexico, *collector unknown s.n.* (holotype, MA not seen).

*Clerodendrum fortunatum* Sessé & Mociño, Fl. Mexic., ed. 2, 2: 151. 1894. TYPE: Mexico, *collector unknown s.n.* (holotype, MA not seen).

*Clerodendrum inermis* Sessé & Mociño, Fl. Mexic. ed. 2, 2: 152. 1894. TYPE: Mexico, *collector unknown s.n.* (holotype, MA not seen).

*Clerodendrum mexicanum* Brandegee, Univ. Calif. Publ. Bot. 3: 39. 1909. TYPE: Mexico, *Purpus 3336* (isotypes, F, MO, NY, US).

Shrub to 5 m tall; branchlets subterete or tetragonal, medullose, puberulent, lenticellate; nodes annulate, often with band of hairs; leaf scars elevated. Leaves decussate-opposite, blades elliptic to lanceolate, 1.5–9 cm long, 0.6–5 cm wide, base acute or cuneate, apex subacuminate, margin entire, glabrous and densely punctate beneath; midrib prominent beneath, secondaries 5–7 pairs; petioles

FIGURE 5. *Clerodendrum ligustrinum* (Jacq.) R. Br. (*Palmer 407*).—A. Habit.—B. Flower.—C. Stamens.—D. Pistil.—E. Fruit.

5–10 mm long, puberulent. Inflorescences supraaxillary or rarely terminal, cymose, the cymes solitary, opposite, 3–7.5 cm long, 2–7 cm wide, usually only 3- or 4-flowered, often twice dichotomous and then 7-flowered, the terminal ones, when present, similar but usually smaller; peduncles 1.5–4 cm long; pedicels 3–10 mm long, puberulent; bracts foliaceous, caducous, bracteoles and prophylls linear, 1–6 mm. Flowers with calyx campanulate, 5–8 mm long, outside puberulent, 5-lobed, lobes lan-

ceolate or deltoid, 3–4 mm long; corolla hypocrateriform, white, outside resinous-punctate, internally slightly pubescent, tube slender, 1–2 cm long, limb 5-lobed, 1–1.3 cm wide, lobes oblong, 3–5 mm long; stamens 4, filaments long-exserted, ca. 2 cm beyond the throat of the corolla tube, 21–23 cm long; ovary oblong, style 2.8–3.1 cm long, equal to the stamens. Fruit drupaceous, subtending calyx cupuliform, subspheric, 8–12 mm long and wide, bilobed, splitting into two-seeded pyrenes at maturity; seeds obovate (Fig. 5).

*Distribution and habitat.* *Clerodendrum ligustrinum* occurs from northern Mexico to Nicaragua (Fig. 1). It is also cultivated as an ornamental in Mesoamerica and other parts of the New World, as well as in the Old World. This species has been reported from roadsides, creek and river banks, marshes and swamps, beach ridge forest, sandy bushy areas, secondary forests, and evergreen or subevergreen forests. It occurs from near sea level to 500 m.

*Vernacular names and uses.* "Arbol sagrado," "itsimte," "moste," "palo blanco cimarrón," and "snake-tree." It is used as an ornamental in Honduras; Sessé & Mociño (1894) and Gibson (1970) reported that the leaves of this species are used in Mexico and Guatemala in native cooking to flavor fish; Del Amo (1979) reported that a leaf infusion is applied to snake-bites; Mendieta & Del Amo (1981) reported this plant as a diuretic, even in the case of kidney stones.

*Note.* There are three species of *Clerodendrum* in Mesoamerica similar to *C. ligustrinum*: *Clerodendrum aculeatum*, *C. molle*, and *C. pittieri*. However, the calyx of *C. ligustrinum* is not pubescent as is the calyx of *C. molle*, nor is it truncate as is the calyx of *C. pittieri*. In addition, the leaf scars in *C. ligustrinum* are not as prominent as in *C. pittieri* and *C. molle*, nor spine-tipped as in *C. aculeatum*. This species was originally described (Jacquin, 1796), in error, as from Mauritius, based on material cultivated in Vienna. The plant may already have been cultivated on Mauritius and erroneously considered to be native by Jacquin. Another possibility is that the material originally came from Mesoamerica, and Jacquin mistakenly believed that it was from Mauritius. According to Harald Riedl, there is not herbarium voucher in W; Jacquin usually did not make herbarium vouchers of cultivated plants. Therefore, the name must be typified by reference to Jacquin's plate 5, figure 1. Fortunately, this illustration in Jacquin (1796) is adequate to establish the identity of this species.

*Selected specimens examined* MEXICO. CAMPECHE: 20 km E of Champotón, 27 Mar. 1982, *Cabrera 2286* (CAS). VERACRUZ: vicinity of Pueblo Viejo, 2 km S of Tampico, 23–31 May 1910 (*Palmer 407*). BELIZE. 5 mi. from Belize city, past international airport, 22 Mar. 1973, *Dwyer 10351* (MO). GUATEMALA. EL PETEN: La Libertad and vicinity, 19 Mar. 1934, *Aguilar 353* (F, MICH). HONDURAS. CHOLUTECA: vicinity of Choluteca, 20 m, 31 Oct.–9 Nov. 1949, *Standley 24599* (F, US). NICARAGUA. LEON: La Paz Centro, Km 59, new highway to León, 50 m, 13 June 1984, *Moreno 24218* (MO).

**12a. Clerodendrum ligustrinum** var. **nicaraguense** Mold., Phytologia 1: 416. 1940. TYPE: Nicaragua, *Chávez 227* (holotype, US).

This variety differs from the typical form of the species by having leaves and axillary cymes usually ternate and the leaf blades puberulent or pubescent beneath.

*Distribution and habitat.* It occurs from Honduras to Panama in dense wet forest, weedy fields, and bordering mangrove swamps, mostly below 900 m.

*Vernacular names and uses.* "Jasmín," and "si me miras te enamora." It is cultivated as an ornamental in Mesoamerica.

*Note.* A specimen from Chiapas, Mexico (*Breedlove 20913*: *C. ligustrinum*), was referred to this variety by Moldenke (1987) but is incorrectly attributed to this taxon.

*Selected specimens examined.* HONDURAS. CORTES: vicinity of La Lima, 30 m, 11–20 Apr. 1947, *Standley & Chacón 7249* (F). NICARAGUA. CHINANDEGA: vicinity of Chichigalpa, 90 m, 12–18 July 1947, *Standley 11488* (F, NY). ZELAYA: region of Braggman's Bluff, without date, *Englesing 120* (NY). COSTA RICA. LIMON: near Lamm Hotel, near sea level, 19 Oct. 1980, *Gómez 6048* (CR). PANAMA. BOCAS DEL TORO: Almirante out along the road to the Bomba, 15 Oct. 1965, *Blum 1350* (DUKE, MO). COLON: along ocean trail between Río Indio and Miguel de La Borda, at sea level, 7 July 1976, *Croat 36888* (MO).

**13. Clerodendrum molle** Kunth, Nov. Gen. Sp. 2: 244. 1817. TYPE: Ecuador, *Bonpland 3837* (holotype and isotype P-HB. 6209. 46: III. 1, microfiche, MO).

Shrub or small tree to 5 m tall; branchlets subterete or tetragonal, medullose, densely short pubescent, lenticellate; leaf scars prominent. Leaves decussate-opposite or ternate, blades elliptic, 1.5–5.5 cm long, 1–2.5 cm wide, base acute, apex acute, puberulent above, short-tomentose beneath, punctate beneath; midrib usually more densely puberulent than the blade above, secondaries 3–6 pairs; petioles 3–8 mm long, pubescent, the lowest

1–2 mm long, persisting as a corky protuberance after the blade has fallen. Inflorescences axillary or terminal, cymes ternate, solitary in each axil, 3–7 cm long, 1–4 cm wide, 3–9-flowered, pubescent; peduncles 1–3.7 cm long, pubescent; pedicels 1–7 mm long, densely pubescent; bracteoles and prophylls linear, ca. 1 mm long, densely pubescent. Flowers with calyx campanulate, 4–7 mm long, pubescent, 5-lobed, lobes ovate, 2–3 mm long; corolla hypocrateriform, white or pinkish, outside pubescent and resinous-punctate, internally slightly pubescent, tube 1.8–2.5 cm long, limb 5-lobed, 1–1.3 cm wide, lobes oblong, 2–3 mm long; stamens 4, filaments long-exserted, ca. 1.5 mm beyond the throat of the corolla tube, 15–20 mm long, anthers oblong; ovary oblongoid; style 3–3.3 cm long, equal to or longer than the stamens. Fruit not seen.

*Distribution.* *Clerodendrum molle* is native from Panama to Colombia, coastal Ecuador, and the Galápagos Islands. In Mesoamerica it is only known from Panama (Fig. 2). It is found mostly on the seashore and at lower elevations, especially on rocky coastline precipices, lava flows, and in open woodland on hillsides, from sea level to less than 500 m.

*Vernacular names and uses.* None reported in Mesoamerica.

*Note.* The Mesoamerican specimen was collected in the late 1700s or earliest 1800s. The specimen label indicates that the specimen was collected in Panama, and that is possible since the species occurs in coastal Ecuador; however, it is also possible that a label mixup occurred and it was actually collected in Ecuador, and not in Panama. There are three Mesoamerican species of *Clerodendrum* that resemble *C. molle* in habit and habitat (see note under *C. ligustrinum*).

*Specimen examined.* PANAMA. PANAMA: *Nee s.n.* (MA).

**14. Clerodendrum aculeatum** (L.) Schldl., Linnaea 6: 750. 1831. *Volkameria aculeata* L., Sp. Pl. ed. 1, 1: 637. 1753. TYPE: Jamaica, *Browne s.n.* (holotype, Linn-809.1, microfiche, MO).

*Clerodendrum aculeatum* var. *grandifolium* Kuntze, Revis. Gen. Pl. 2: 505. 1891. TYPE: St. Thomas, *collector unknown s.n.* (holotype, NY not seen).

Shrub to 2.5 m tall; branches, branchlets, and twigs subterete or tetragonal, medullose, appressed-pubescent, lenticellate, spinose; spines 2–7 mm long, ternate or opposite, borne on and subtending the nodes. Leaves decussate-opposite, ternate, or apically clustered, on the upper side of a spine; blade elliptic or lanceolate, 1–4 cm long, 0.3–1 cm wide (sometimes larger and wider in the West Indies), base acute or cuneate, usually mucronulate, glabrous on both surfaces, punctate beneath due to deeply sunken resinous peltate glands; midrib prominulous beneath, secondaries 3–7 pairs; petioles of the primary leaves with a very stout, ligneous spinescent base, 3–11 mm long, eventually breaking off obliquely ⅓ to ½ the distance from apex to base, the base persisting as a sharp, subulate-tipped spine, petioles of the small axillary leaves obsolete or very short and not spinescent. Inflorescences axillary, pedunculate, crowded at the apex or upper nodes of the branchlets and twigs, cymes solitary, 2–6 cm long, 1.5–3.5 cm wide, 3–7-flowered; peduncles 1–3.5 cm long, puberulent; pedicels 2–10 mm long, puberulent; bracts linear. Flowers cymose, slightly zygomorphic; calyx tubular or campanulate, 3–7 mm long, outside, usually pubescent, 5-lobed, lobes ovate, 2–3 mm long; corolla hypocrateriform or infundibular, white, outside resinous-punctate, inside slightly pubescent, tube slender, 1.3–2.3 cm long, limb 5-lobed, 1–1.5 cm wide, lobes oblong, 5–8 mm long, shorter than the tube; stamens 4, filaments much exserted, 2–3 cm long; ovary minute, style 3–3.2 cm long, much exserted and equal to the stamens. Fruit drupaceous, subtending calyx cupuliform, 5–10 mm long and wide, in age 4-lobed, splitting in 2-seeded pyrenes; seeds oblong; chromosome number: $n = 12$ (Cave, 1959, 1964).

*Distribution and habitat.* *Clerodendrum aculeatum* occurs in the West Indies from the Bahamas south to Barbados. It is planted and sometimes naturalized from Veracruz (Mexico) south to northern South America, and in the Old World (Moldenke, 1980). In Mesoamerica, it is known only from the Swan Islands, off Honduras, which is the first report for the species in Mesoamerica. It is often locally abundant and occurs in open grassland, dry scrub, limestone, swamplands, and beachside areas, mostly from sea level to 500 m.

*Vernacular names and uses.* None are reported in Mesoamerica. *Clerodendrum aculeatum* is used in living fencerows and medicinally in cases of gonorrhea; a decoction of the leaves is used as a cough remedy (Reis & Lipp, 1982).

*Note.* This species closely resembles *C. inerme* of Asia, *C. ligustrinum* and *C. pittieri* from Mesoamerica, and *C. molle* and *C. ternifolium* of South America in habit and habitat. However, *C. aculeatum* differs from these species in the very

sharp-tipped spine at the nodes. According to Fred Barrie, the Linnaeus specimen number 809.1 is the same specimen named by Browne (1756) "*Clerodendrum fruticosum, spinosum; foliis inferioribus confertis, superioribus oppositis; pedunculis tripartitis, trifloris, alaribus.*" Apparently, Linnaeus never saw actual material of this species until after he had published his binomial based on Browne's material mentioned above. Therefore, specimen 809.1, although not sent by Browne to Linnaeus until 1756, is presumably the basis for Browne's polynomial and for Linnaeus's epithet. Specimen 809.2, also identified as *Volkameria aculeata*, lacks spines and is probably *C. inerme* rather than *C. aculeatum*.

*Specimens examined.* HONDURAS. SWAN ISLANDS: Great Swan Island, surroundings of the military base, 17 May 1980, *Cruz & Espinal 263* (TEFH); without precise locality, 15–24 Aug. 1971, *Proctor 32509* (IJ, TEX); tropical wet forest, at sea level, 10 June 1986, *Nelson et al. 9770* (TEFH).

**15. Clerodendrum pittieri** Mold., Phytologia 1: 416. 1940. TYPE: Panama, *Pittier 4965* (holotype, US; isotype, F, MO).

Shrub to 3 m tall; branches and branchlets tetragonal, slightly flat at the nodes, medullose, with appressed hairs, lenticellate; leaf scars spinescent but not sharp-tipped. Leaves decussate-opposite, ternate, or sometimes clustered on reduced axillary twigs; blade lanceolate to elliptic, 0.7–4 cm long, 0.3–2.5 cm wide, base acute or cuneate, apex acute or obtuse, densely punctate beneath; midrib prominent beneath, secondaries 3–7 pairs; petioles with a ligneous subspinescent base, 1–8 mm long, eventually breaking off obliquely 1–2 mm from the base, the petioles of the axillary clustered leaves obsolete or very short and not spinescent. Inflorescences axillary, at the upper nodes of branchlets and twigs, cymes solitary at the axils of the spines, 3–5 cm long, 1.5–3.5 cm wide, 1–3-flowered; peduncles 0.7–2 cm long, with appressed hairs; pedicels 0.5–1.2 cm long, subglabrate; prophylls linear-subulate, 1–2 mm long. Flowers with calyx campanulate, 2–4 mm long, puberulent, truncate, 5-dentate; corolla hypocrateriform, white or tinged pink-purple, puberulent, internally slightly pubescent, tube 1.5–2.2 cm long, limb 5-lobed, lobes oblong or elliptic, 4–8 mm long; stamens 4, filaments much exserted, 2.3–2.5 cm long; ovary oblong, style 3.3–3.6 cm long, much exserted, equal to or shorter than the stamens. Fruit drupaceous, subtending calyx cupuliform, obovate, 5–13 mm long and wide, bilobed, splitting into two 2-seeded pyrenes at maturity; seeds oblong.

*Distribution and habitat.* *Clerodendrum pittieri* occurs from Guatemala to Ecuador and Venezuela. All the Mesoamerican collections are from the Pacific Coast (Fig. 3). The occurrence of *C. pittieri* on the Atlantic Coast is restricted to Colombia and Venezuela. This species is usually found in mangrove areas, dry forested hills above mangroves, salt flats, around tidal pools, and on riverbanks near saltwater. It is common in Nicaragua, in the mangrove forest of Poneloya (León) and Puerto Morazán (Chinandega) (pers. obs.).

*Vernacular names and uses.* "Espino." No uses reported.

*Note.* *Clerodendrum pittieri* closely resembles three other Mesoamerican species of *Clerodendrum* (see note under *C. ligustrinum*). The name was used for the first time by Standley in 1938, but was validly published by Moldenke in 1940.

*Selected specimens examined.* GUATEMALA. ESCUINTLA: near San José, at sea level, 30–31 Jan. 1939, *Standley 63974* (F). SAN MARCOS: Ocós, 1–2 m, 15 Mar. 1940, *Steyermark 37854* (F). COSTA RICA. GUANACASTE: Puerto Jesús on the Gulf of Nicoya ca. 13 km E of La Mansión, 20 July 1981, *Wilbur 31775* (DUKE). PUNTARENAS: Pacific Coast, banks between Los Loros and Tivines, 17–26 Feb. 1938, *Brenes 22671* (F, NY). PANAMA. CHIRIQUÍ: vicinity of David, 30 80 m, 30 Mar. 1911, *Pittier 3374* (F, US). COCLE: Aguadulce, near sea level, 3–6 Dec. 1911, *Pittier 4965* (F, MO, US).

## EXCLUDED TAXA

*Clerodendrum epiphyticum* Standley, Field Mus. Pub. Bot. 22: 168. 1940 (as "*Clerodendron*") = *Gibsoniothamnus epiphyticus* (Standley) L. O. Williams (Bignoniaceae), Field Mus. Pub. Bot. 34: 120. 1972.

*Clerodendrum mutadae* Standley, Field Mus. Pub. Bot. 17: 206. 1937 (as "*Clerodendron*") = *Aegiphila costaricensis* Mold., Fieldiana, Bot. 24: 170. 1970.

*Clerodendrum moldenkeanum* Standley, Field Mus. Pub. Bot. 22: 99. 1940 (as "*Clerodendron*") = *Gibsoniothamnus moldenkeanus* (Standley) L. O. Williams (Bignoniaceae), Fieldiana, Bot. 32: 214. 1970.

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*Clerodendrum standleyi* Moldenke, Geogr. Distrib. Members Verbenac. Avicenniac., 76. 1942 = *Trybliocalyx pyramidatus* Lindau (Acanthaceae), Bull. Herb. Boissier, ser 2, 4: 328. 1904.

*Clerodendrum mimicum* Standley & Steyerm., Field Mus. Pub. Bot. 23: 227. 1944 (as "*Clerodendron*") = *Gibsoniothamnus mimicus* (Standley & Steyerm.) L. O. Williams (Bignoniaceae), Fieldiana, Bot. 32: 214. 1970.

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# POLLEN DEVELOPMENT AND FERTILIZATION IN *LACANDONIA SCHISMATICA* (LACANDONIACEAE)[1]

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## Abstract

The flower of *Lacandonia schismatica* is bisexual. Three or sometimes four bilocular or trilocular anthers occupy the center of the flower inside the zone of carpels. The anther wall comprises four layers: epidermis; endothecium whose cells develop helical wall thickenings; one middle layer, which disappears early; a tapetum of the secretory type. The tapetal cells apparently form cytoplasmic bridges among themselves. The microspore tetrads are in an isobilateral arrangement, surrounded by a thick wall. The mature anther wall has only two cell layers: epidermis and endothecium. The pollen grain is three-celled by the time germination occurs. Anther dehiscence has not been observed and probably does not occur.

Pollination of *Lacandonia schismatica* occurs in the unopened flower bud. The pollen grains germinate within the anthers, which do not dehisce, and the pollen tubes grow within the receptacle until they reach the ovules. The pollen tube enters the embryo sac through the micropyle and one synergid, and fertilization is completed by anthesis. This reproductive pattern conforms to Lord's definition of preanthesis cleistogamy.

*Lacandonia schismatica* E. Martínez and C. H. Ramos is endemic to shady sites in a rainforest of southeastern Mexico. It is a saprophyte, and flowers all year if moisture is adequate. Flowering is especially abundant in November and December, after the rainy season (Martínez & Ramos, 1989).

*Lacandonia schismatica* has been proposed as a new monotypic family, the Lacandoniaceae (order Triuridales) (Martínez & Ramos, 1989). It is closely allied to the Triuridaceae (see the description in Maas & Rübsamen, 1986); in fact, it has been proposed that the genus be included in the Triuridaceae (Rübsamen-Weustenfeld, 1991).

The position of the androecium inside the zone of carpels makes the flower unique in angiosperms and gives room for more speculation about the origin of the flower and of the Triuridales. Otherwise, the reproductive structures of *L. schismatica* (Márquez-Guzmán et al., 1989; Martínez & Ramos, 1989) are comparable to those mentioned for the Triuridaceae to which *Lacandonia schismatica* is most closely related (Tomlinson, 1982; Maas & Rübsamen, 1986; Rübsamen-Weustenfeld, 1991).

On the other hand, its uniqueness makes one wonder if the structure is homologous to flowers in other angiosperms (Stevens, 1991). This paper is a report of continuing studies on the reproductive anatomy of *L. schismatica* (see Márquez-Guzmán et al., 1989). We analyze here the development of the anther, the formation of the pollen grains, some aspects of their germination and observations on the fertilization, an aspect of special interest in this monotypic family, unique in the flowering plants. Supplementing data on microsporogenesis is provided by Davidse & Martínez (1990).

## Materials and Methods

Flowers in anthesis, older flowers, and flower buds of different ages were fixed at the site of collection in the Lacandona forest, Chiapas, Mexico. They were collected in January and August 1990. Three fixatives were employed: (a) FAA (5% formalin + 5% acetic acid + 63% ethanol + 27% water); (b) glutaraldehyde (5% glutaraldehyde + 0.25 M sucrose + 0.1 M phosphate buffer, pH 6.8); (c) glutaraldehyde paraformaldehyde (5% glutaraldehyde + 4% paraformaldehyde + 0.1 M s-collidine, pH 7.2). The material fixed in FAA was embedded in paraffin. The sections (8–10 μm) were mounted in 0.005% aniline blue for fluorescence micros-

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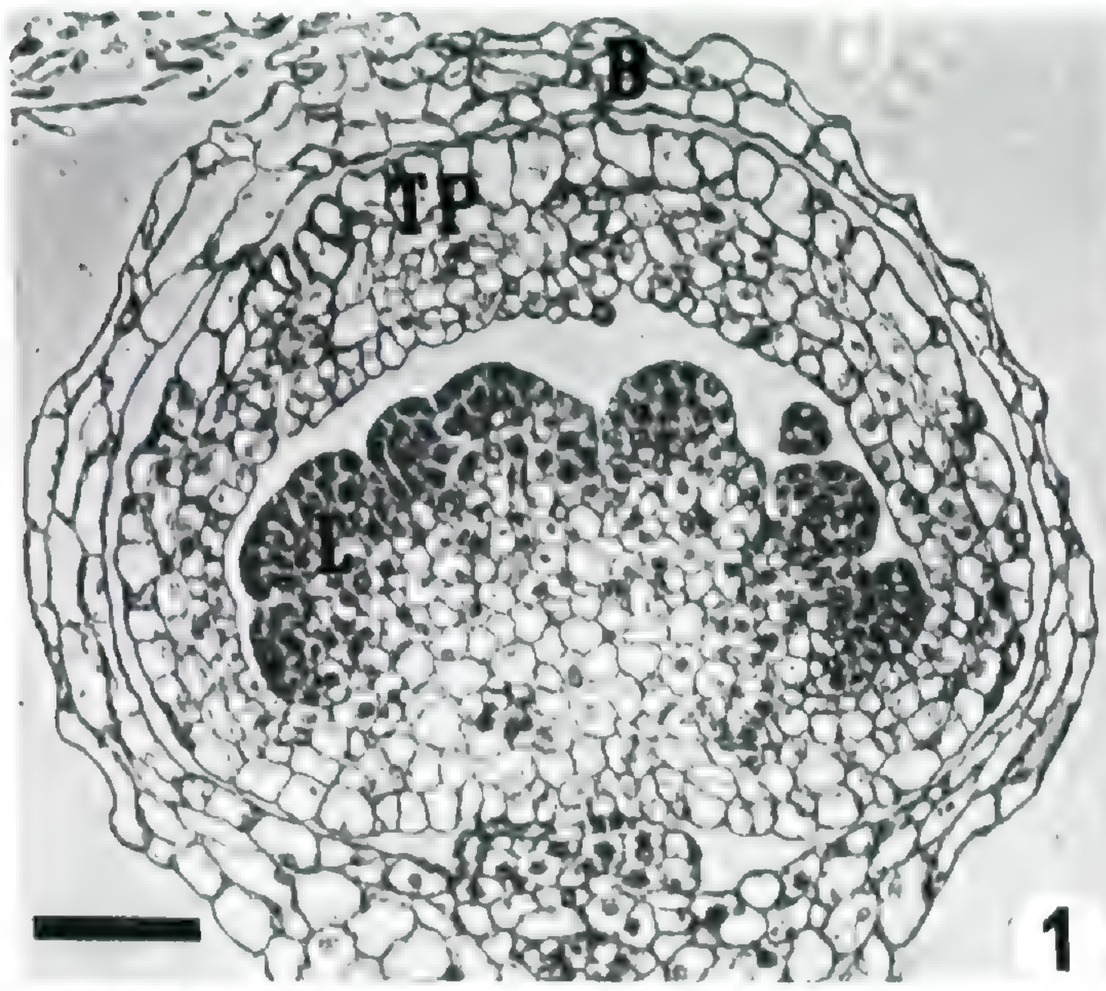
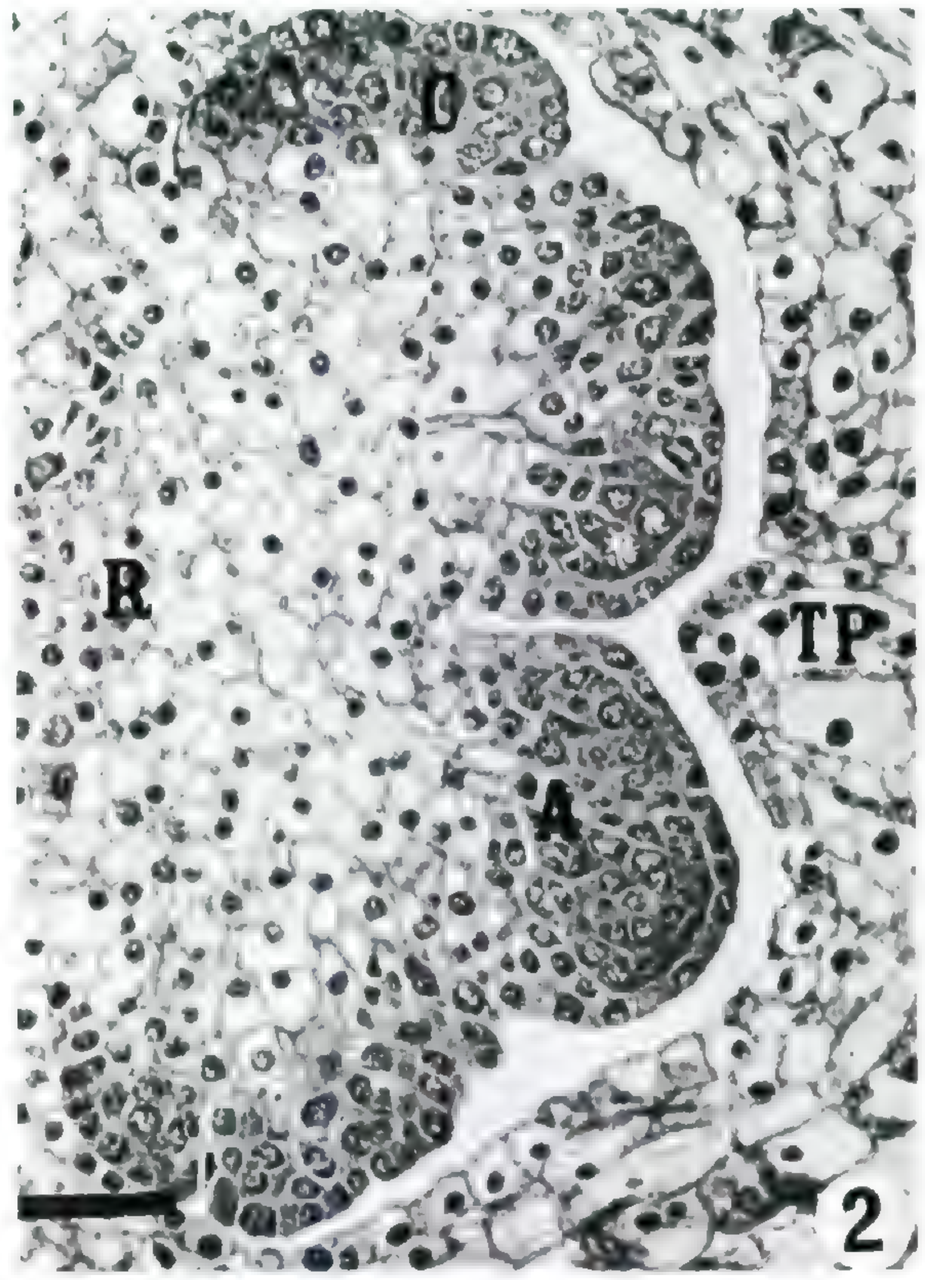
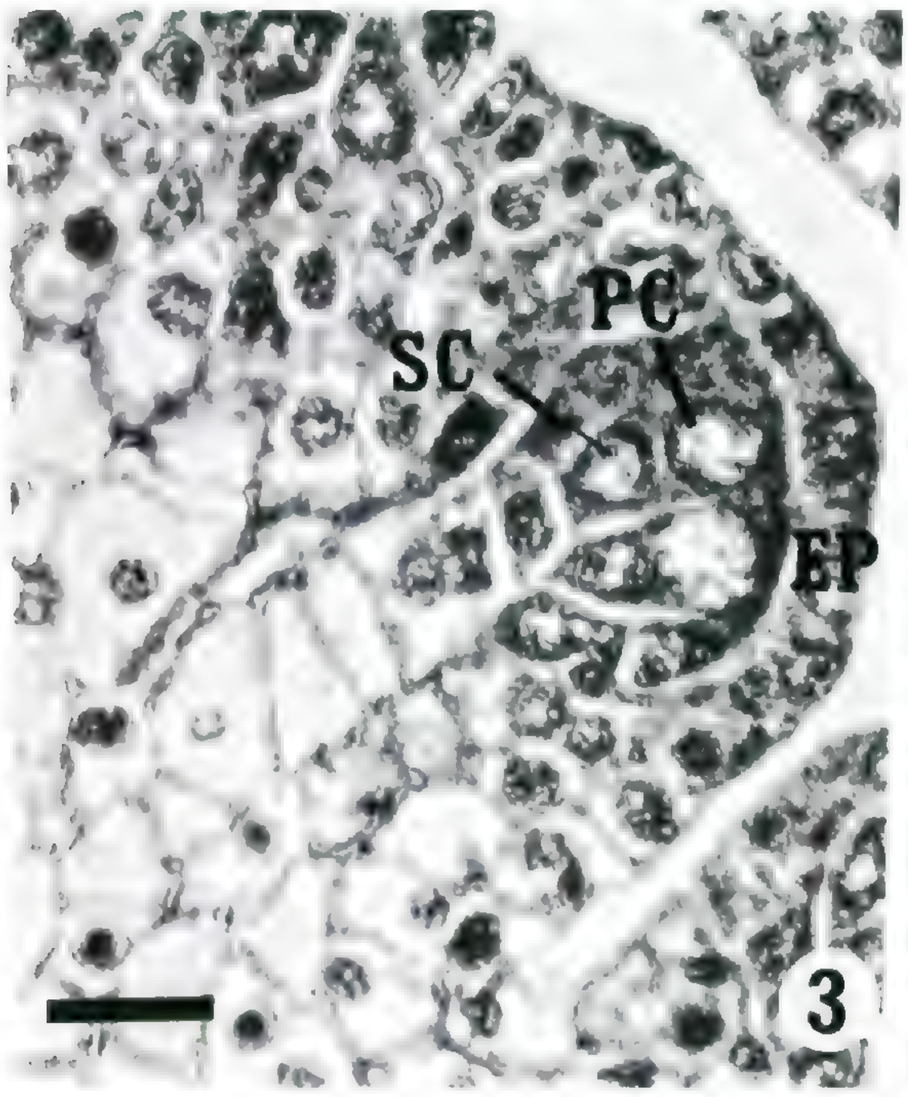
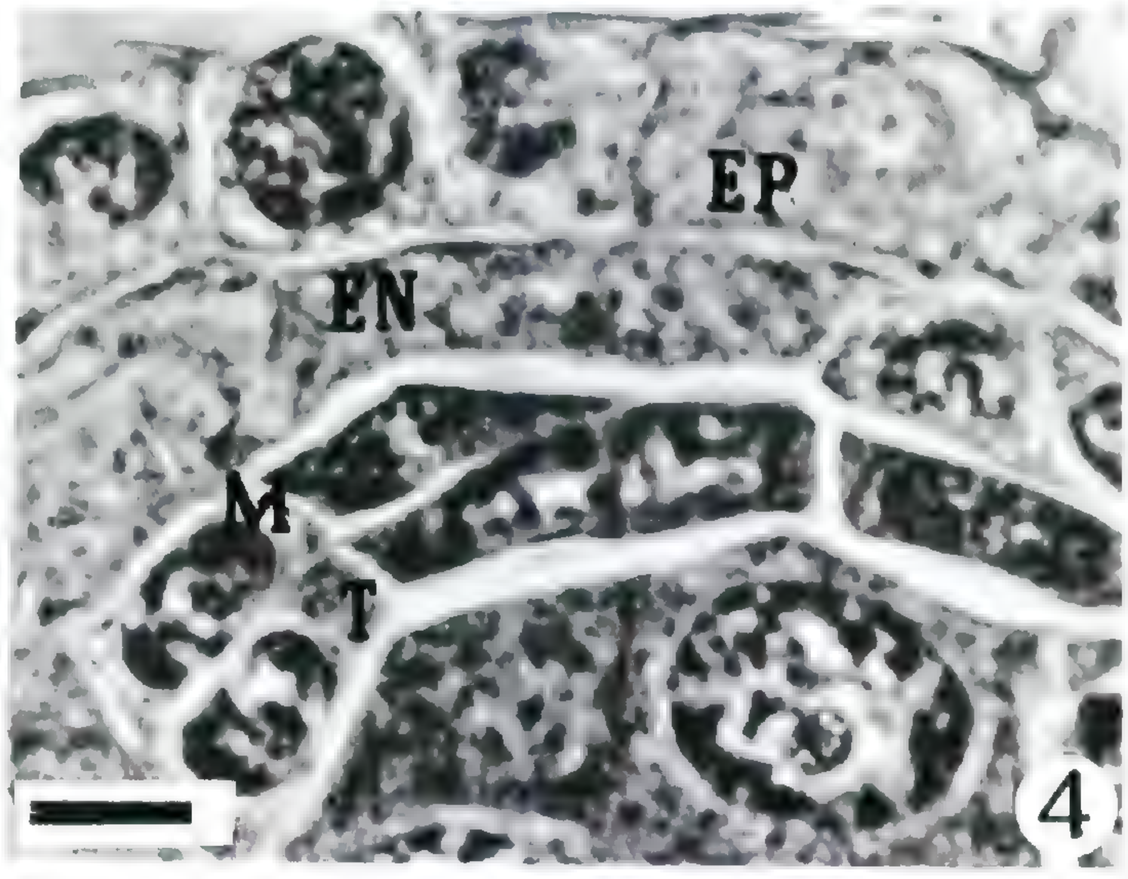
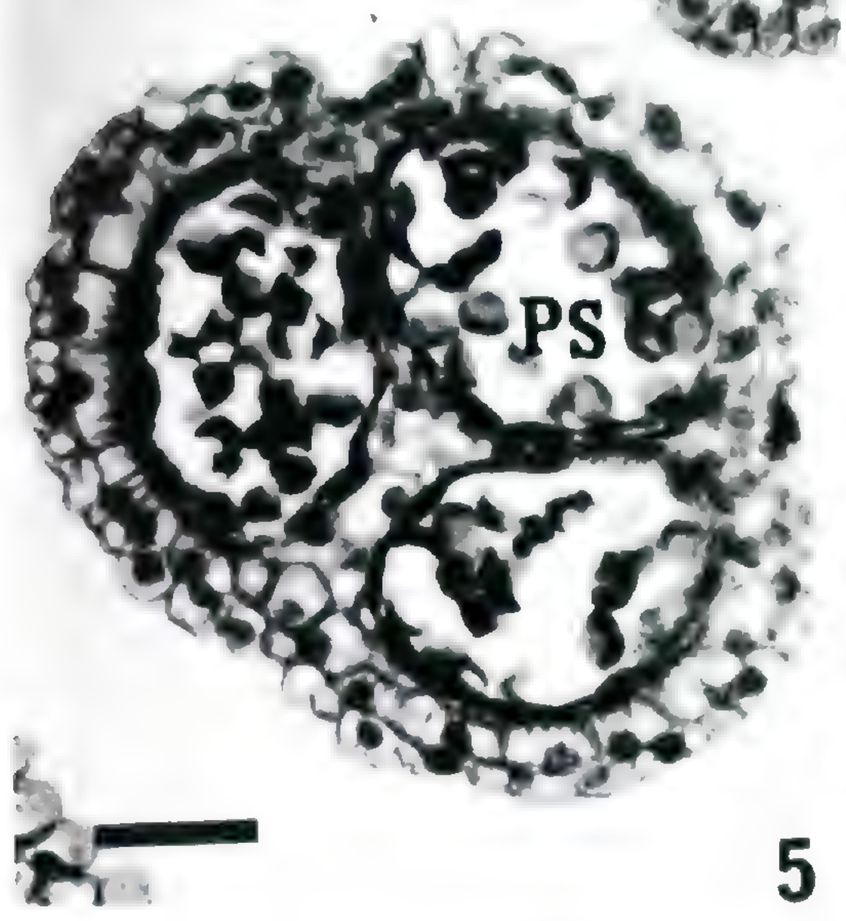
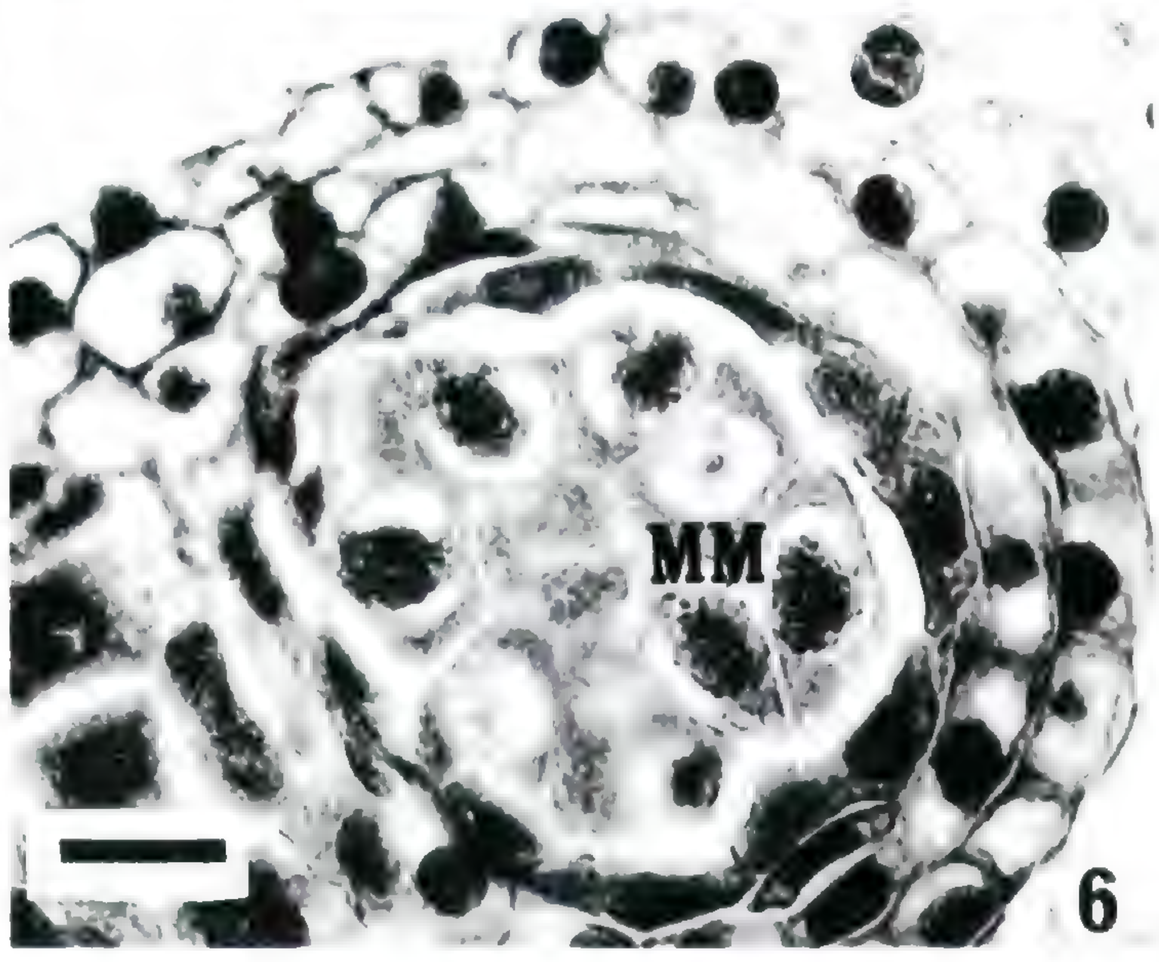



FIGURES 1–6. Anther development—1. Longisection of the floral bud, scale bar = 250 μm.—2. Longisection of the floral bud showing primordia of the sessile anthers, scale bar = 150 μm. –3. Longisection of the young anther showing periclinal division of an archesporial cell, scale bar = 63 μm.—4. Transection of the anther wall at microspore mother cell stage, scale bar = 25 μm.—5. Transection of the anther with three pollen sacs, scale bar = 156 μm.—6. Transection of the young anther showing microspore mother cells in meiosis, scale bar = 62 μm. A, anther; B,

copy. The material fixed in glutaraldehyde was dehydrated in acetone and embedded in JB-4 plastic mixture. Sections were cut at 1–2 μm. They were stained with toluidine blue. The third fixative was followed by postfixation in osmium tetroxide. After alcohol dehydration, the tissues were embedded in Epon 812. They were cut at 1–2 μm and stained with toluidine blue. Additionally, fine sections were examined by transmission electron microscopy.

## Results

*Lacandonia schismatica* is a specialized saprophyte. Perfect flowers are produced on its aerial shoots. The gynoecium consists of 60–80 papillose carpels. Each carpel surrounds a basal sessile ovule that is anatropous and bitegmic. The inner integument forms the micropyle. The androecium consists of three or sometimes four bilocular anthers with introrse stomia. The mature pollen grains contain three cells (Márquez-Guzmán et al., 1989; Martínez & Ramos, 1989).

When the tepals have finished development, the floral meristem begins to form lobes (Fig. 1). As the lobes grow, the central ones become recognizable as primordia of the sessile anthers in the center of the flower. They also are larger than the surrounding lobes that will form the carpels (Fig. 2).

In the anthers some of the subprotodermal cells elongate perpendicularly to the surface. These become the archesporial cells. Two cells result from a periclinal division of an archesporial cell (Fig. 3). The internal one (the sporogenous cell) divides repeatedly and forms the sporogenous tissue. The outer one (the parietal cell) divides twice to form the endothecium, a single intermediate layer, and the tapetum (Fig. 4). Sterile cells in the sporogenous zone divide the anther into two or rarely three pollen sacs (Fig. 5).

After the anther wall cells have completed division, the microspore mother cells begin meiosis (Fig. 6). At this time the anticlinal and internal walls of the tapetum disappear. The tapetal cells are at their maximum size and protoplasmic content; the nuclei are large. The tapetal cells apparently form cytoplasmic bridges among themselves (Fig. 7). After meiosis, the microspore tetrads are in an isobilateral arrangement as a result of successive cytokinesis, and they are surrounded by callose walls (Fig. 8).

At the time of separation of the microspores, they are still surrounded by a thick wall. The tapetum seems to be functional and some of its cells are binuclear (Fig. 9). During development of the pollen grains, the intermediate layer and the tapetum disappear (Fig. 10).

By the time pollen grains are mature, the endothecium has helical wall thickenings. These thickenings taper off to nothing as they approach the external wall (Fig. 11). The bands of thickening are sometimes connected at the edges of the internal wall. Thus, the internal wall is traversed by the bands, but not by a plate of secondary wall. The epidermis persists to maturity.

We have observed an apparently new phenomenon in at least eight flowers in anthesis: the anthers did not dehisce and the pollen grains germinated within the pollen sac.

The development of the anther is precocious with respect to the carpels (Fig. 12). The male gametophytes mature before the female ones. By the time pollen grains in unopened buds are at the three celled stage (Fig. 13), the carpels are usually in early stages of development. However, the ovules and embryo sacs continue to develop until, before the flower opens, the megagametophyte has seven cells and the egg apparatus is located at the micropylar end, next to the receptacle (Fig. 14).

At this stage, the first signs of germination were observed in the pollen grains inside the unopened anthers (Fig. 15). The resultant pollen tubes grow toward the base of the anther, which is united to the receptacle (Fig. 16). The pollen tubes grow through the receptacle (Fig. 17) to reach the carpels (Fig. 18). They enter the ovule via the micropyle and then penetrate the embryo sac through one synergid (Fig. 19). When the flowers open, fertilization already has occurred, and only the pollen walls (Fig. 20) remain in the unopened anthers.

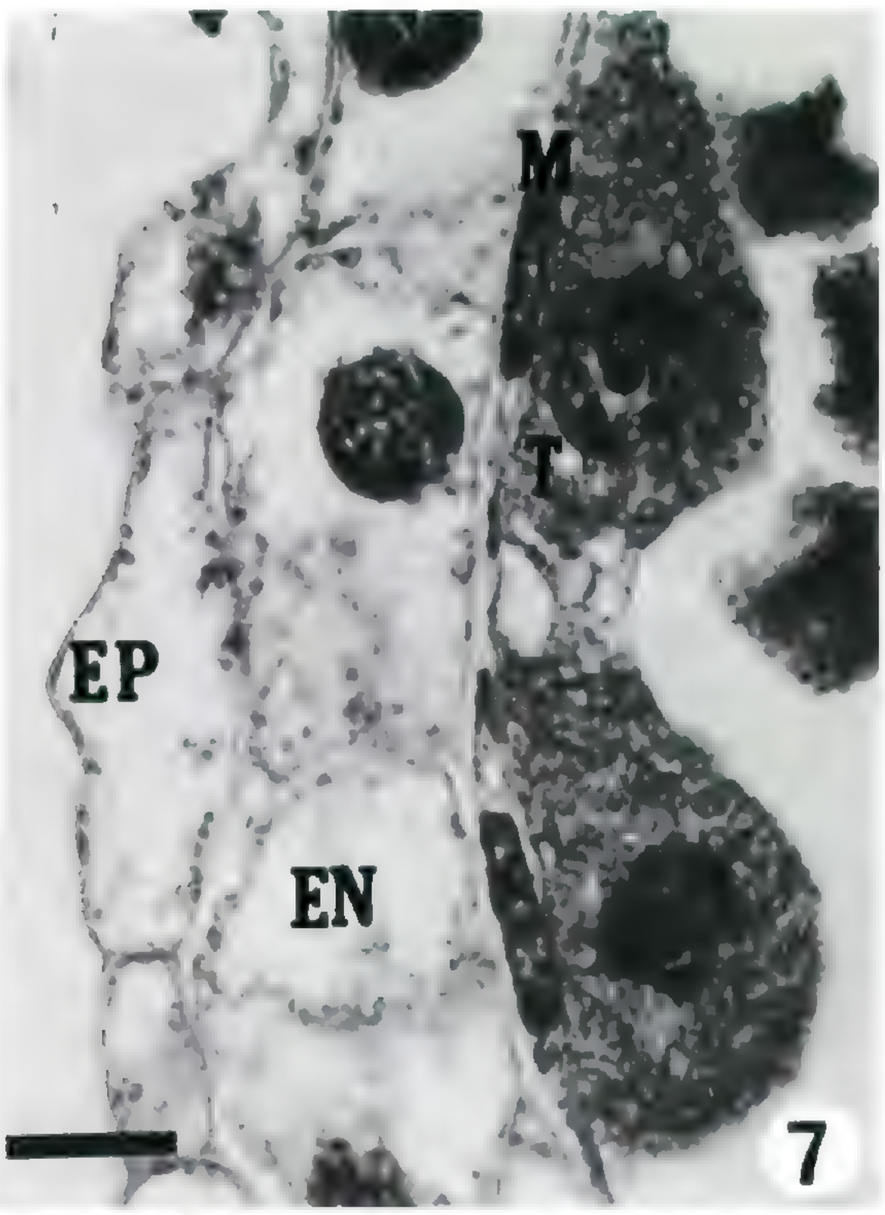
Dehiscence of the anthers does not occur, nor have we seen pollen tubes growing through the anther walls. Pollen grains have not been detected outside the anthers, neither in sections of flower buds nor in images of scanning electron microscopy of open flowers.

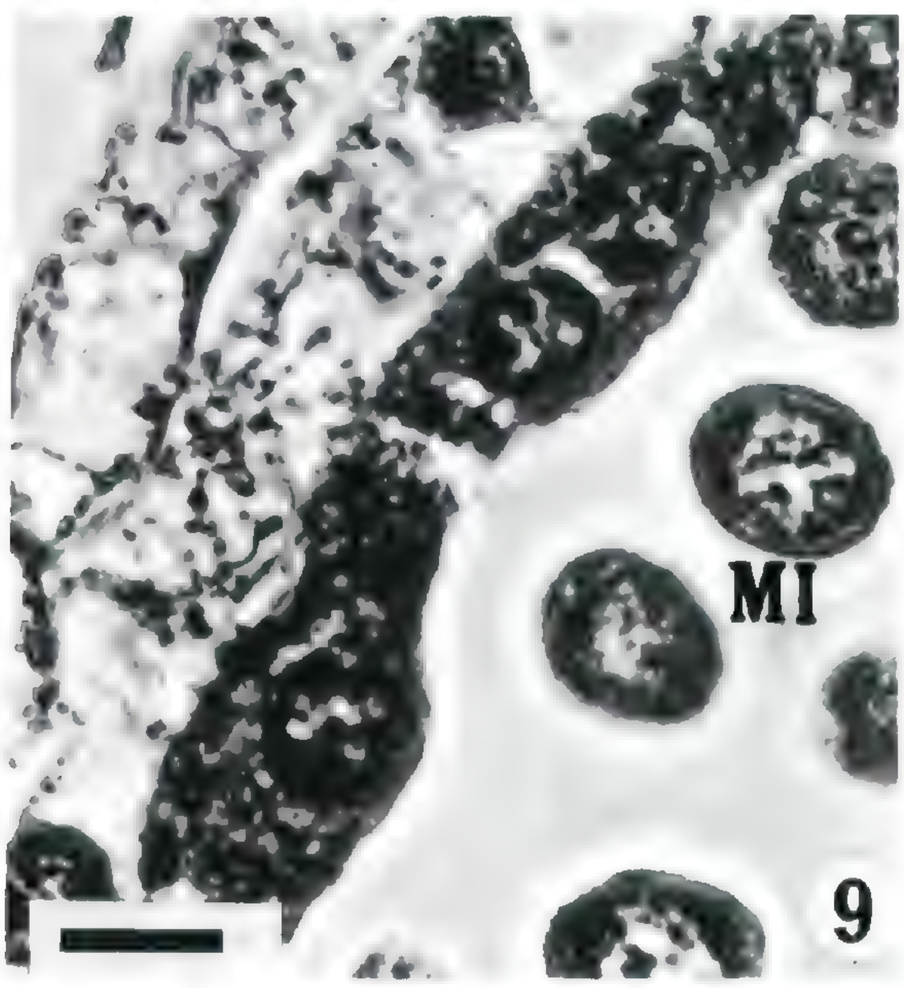
## Discussion

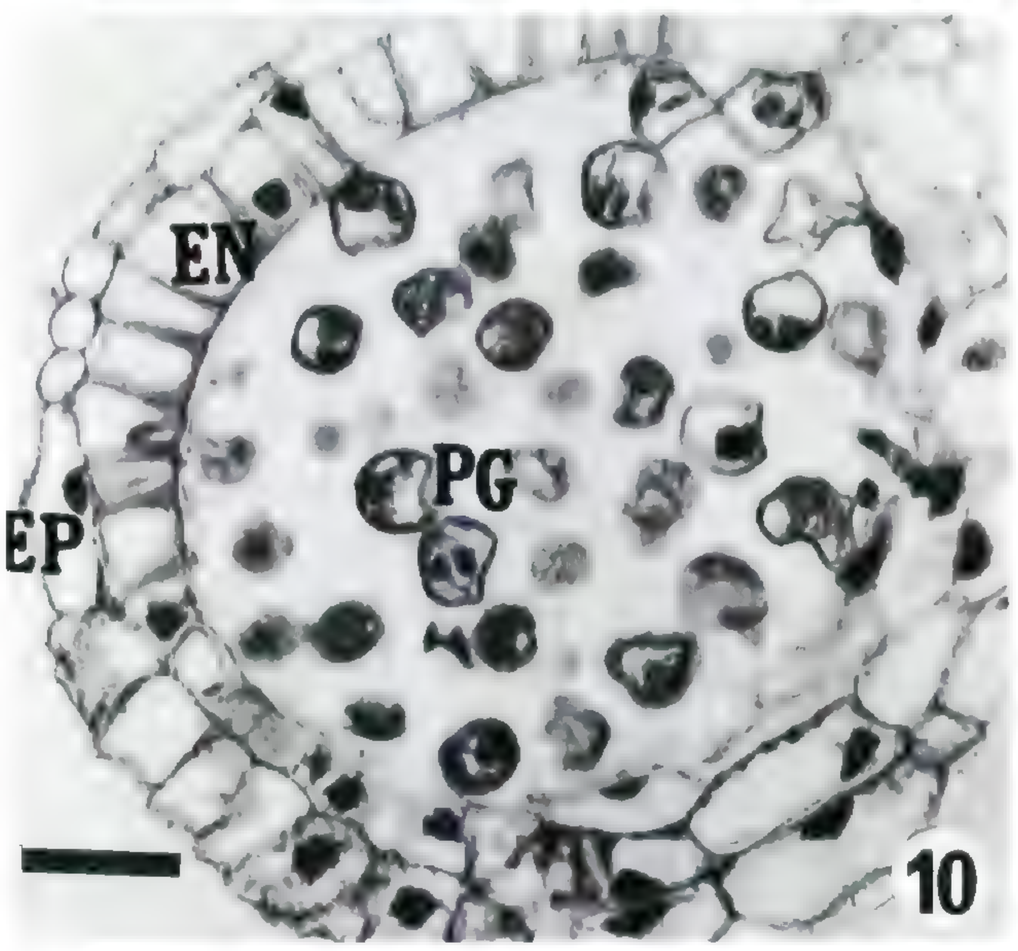
*Lacandonia schismatica* shares many characters with the Triuridaceae (Maas & Rübsamen,

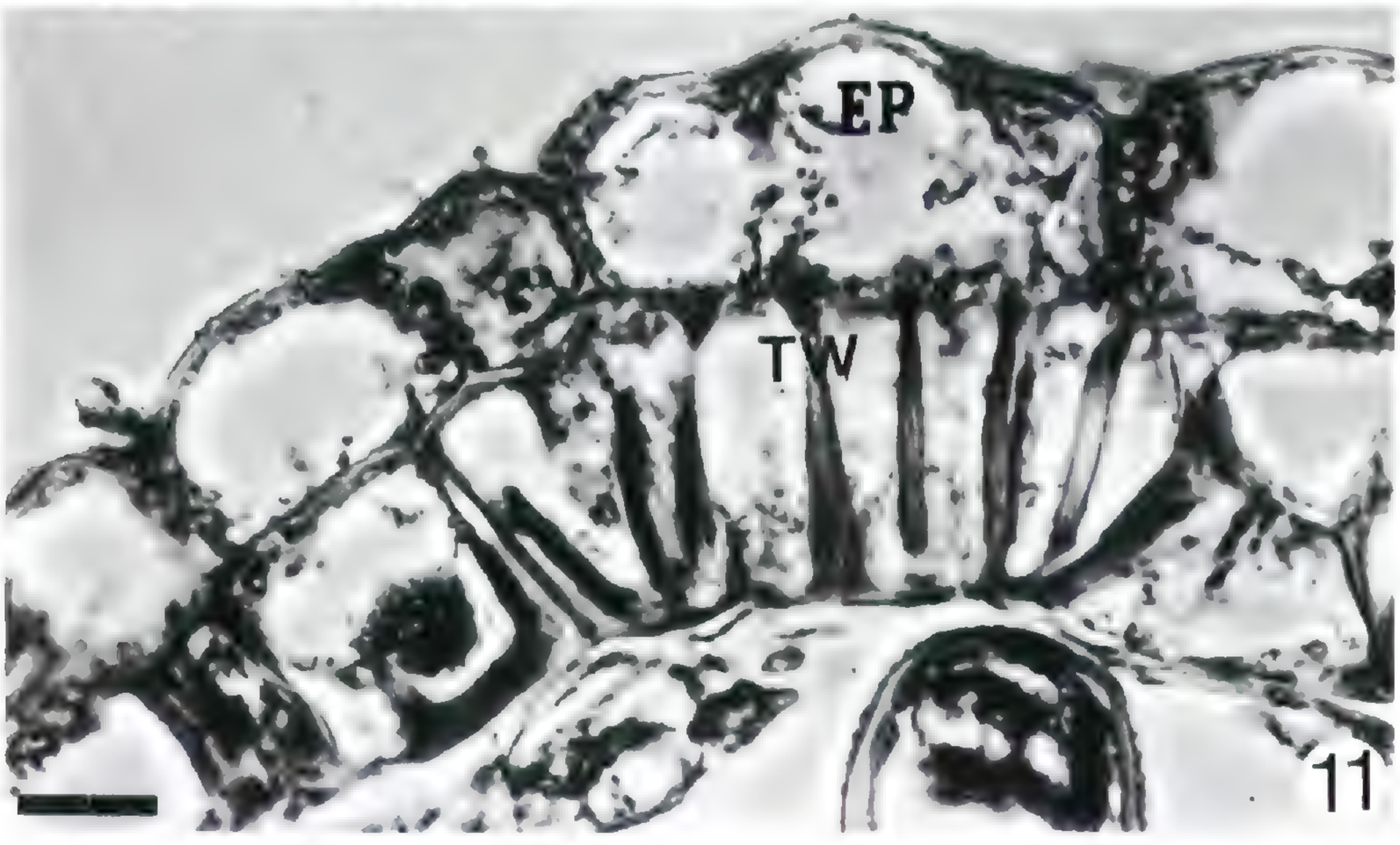
←

bract; C, carpel; EP, epidermis; L, lobes; MM, microspore mother cells; PC, parietal cell; PS, pollen sac; R, receptacle; SC, primary sporogenous cell; TP, tepals.

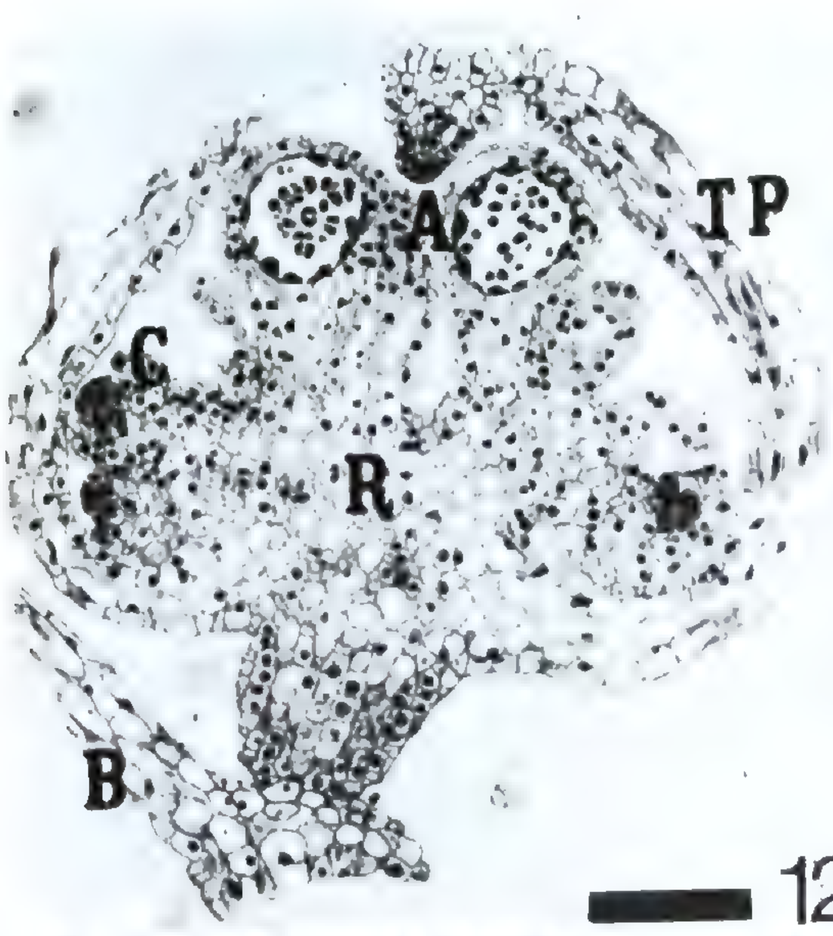





FIGURES 7–11. —7. Apparent cytoplasmic bridges among tapetal cells, scale bar = 25 μm.—8. Microspore tetrads, scale bar = 63 μm.—9. Microspores surrounded by a thick wall, scale bar = 25 μm.—10. Longisection of the mature anther, scale bar = 100 μm.—11. Anther wall with epidermis and fibrous thickenings in endothecium, scale bar = 20 μm. EN, endothecium; EP, epidermis; M, middle layer; MI, microspore; MT, microspore tetrads; PG, young pollen grains; T, tapetum; TW, wall thickenings.

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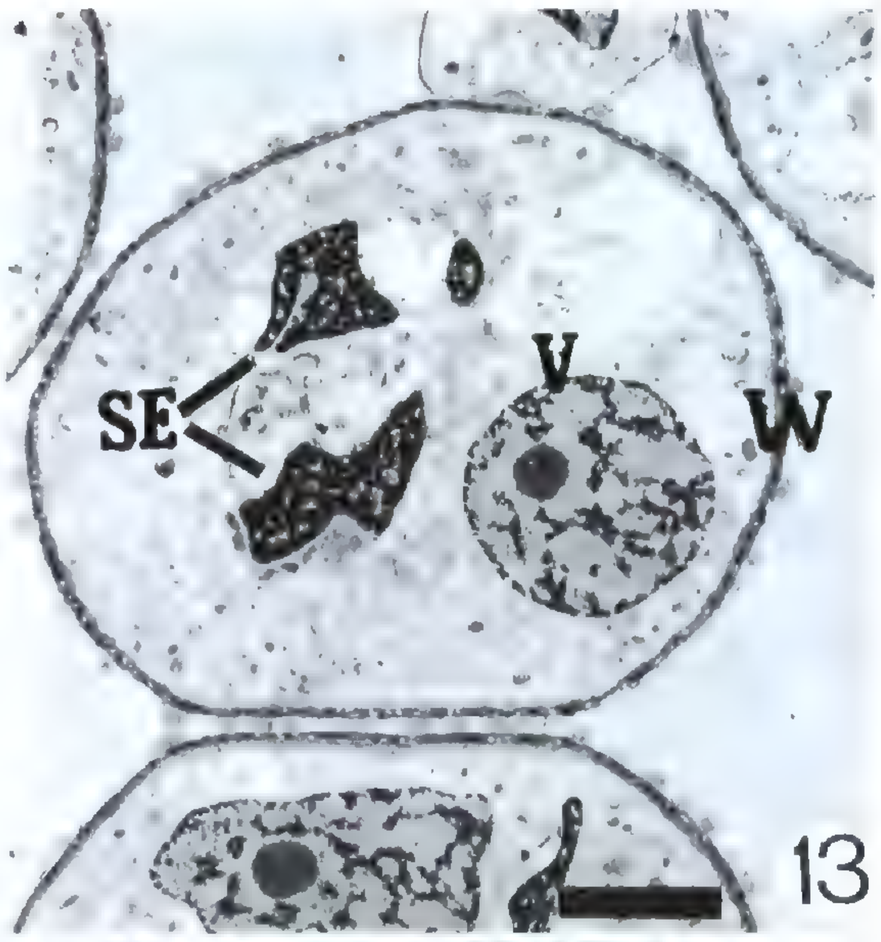


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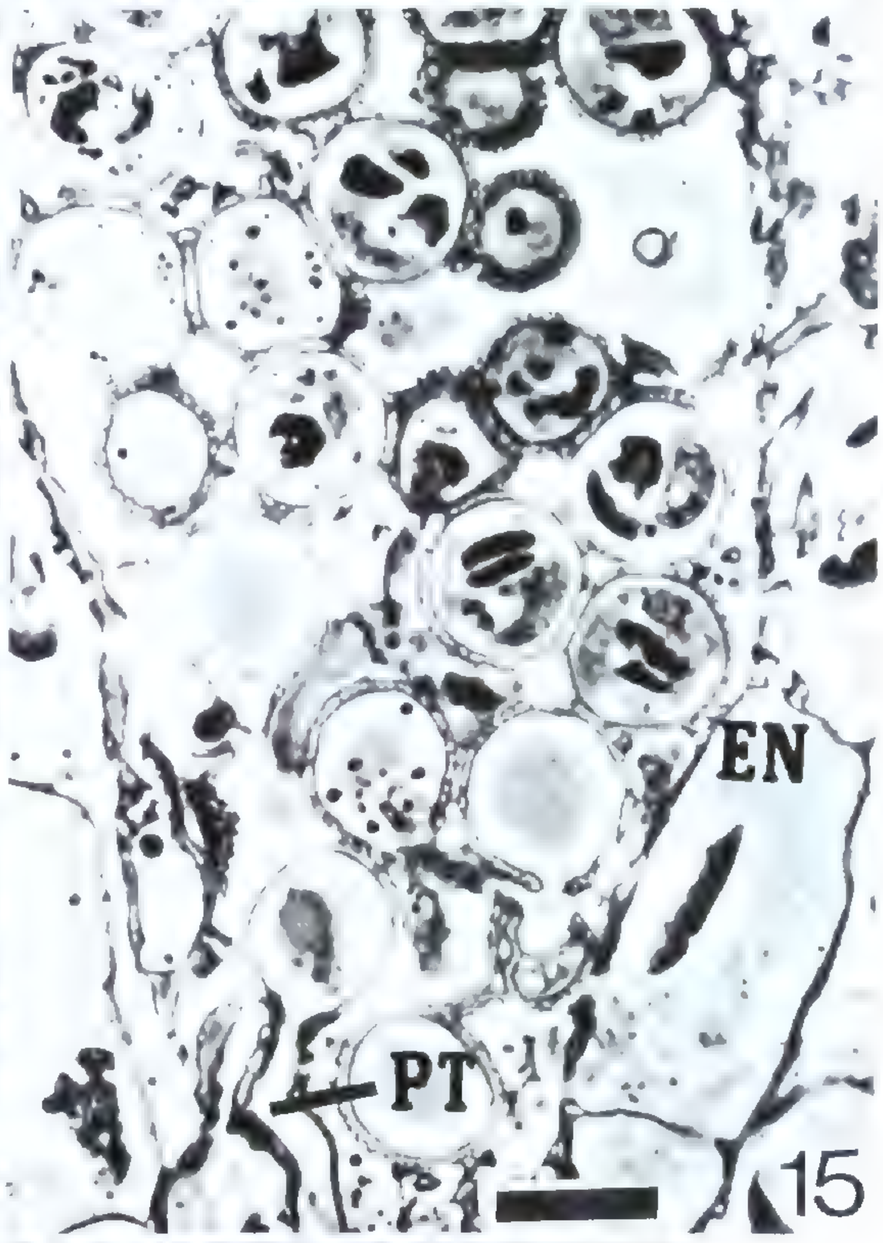


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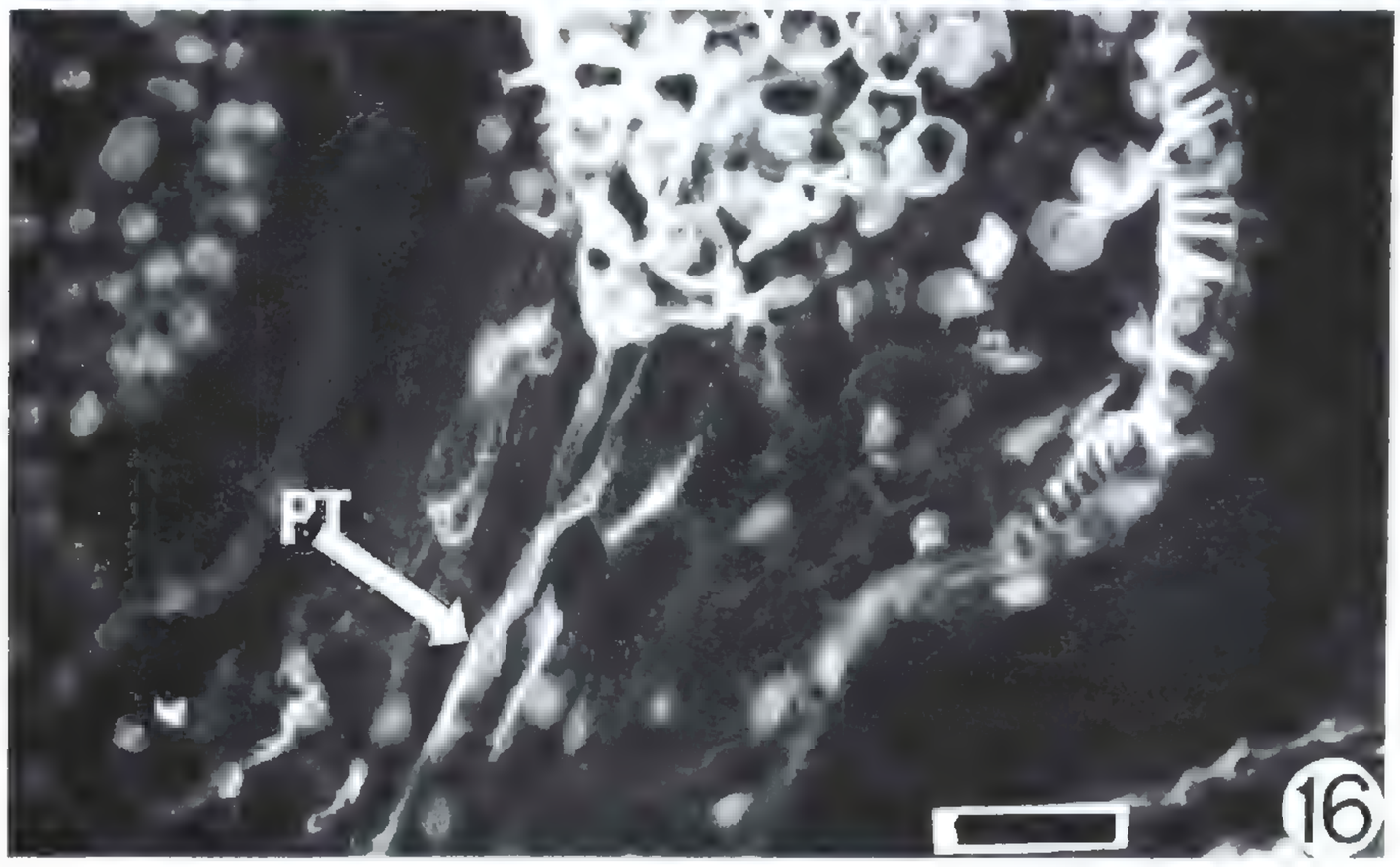


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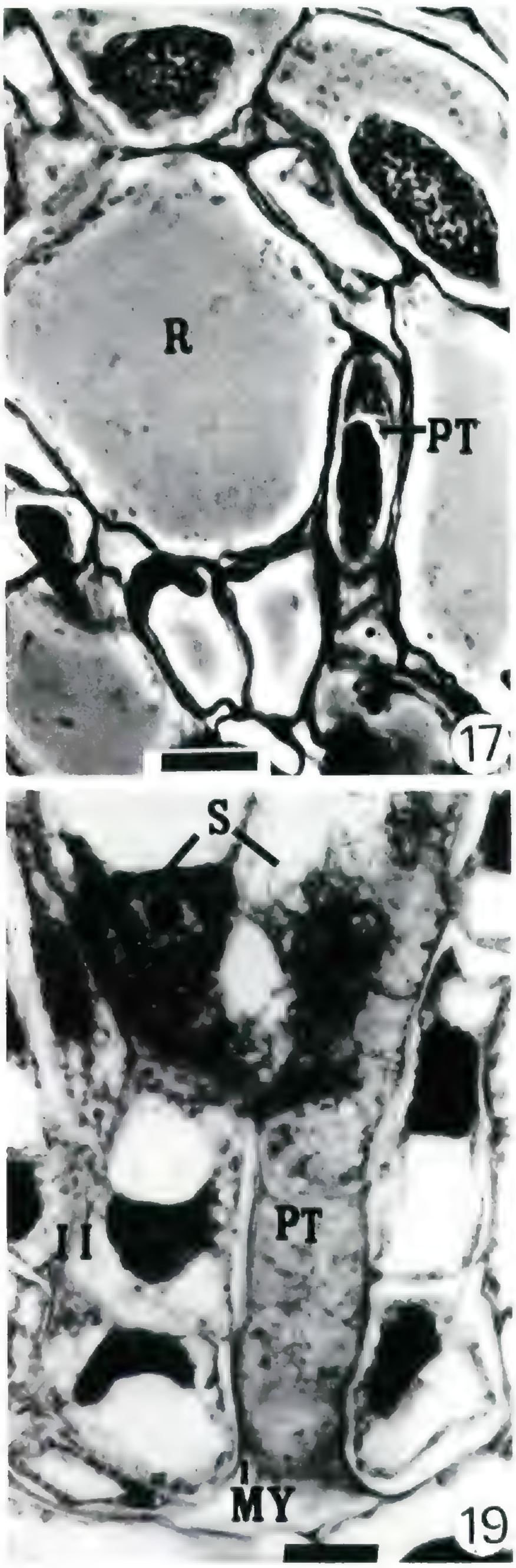
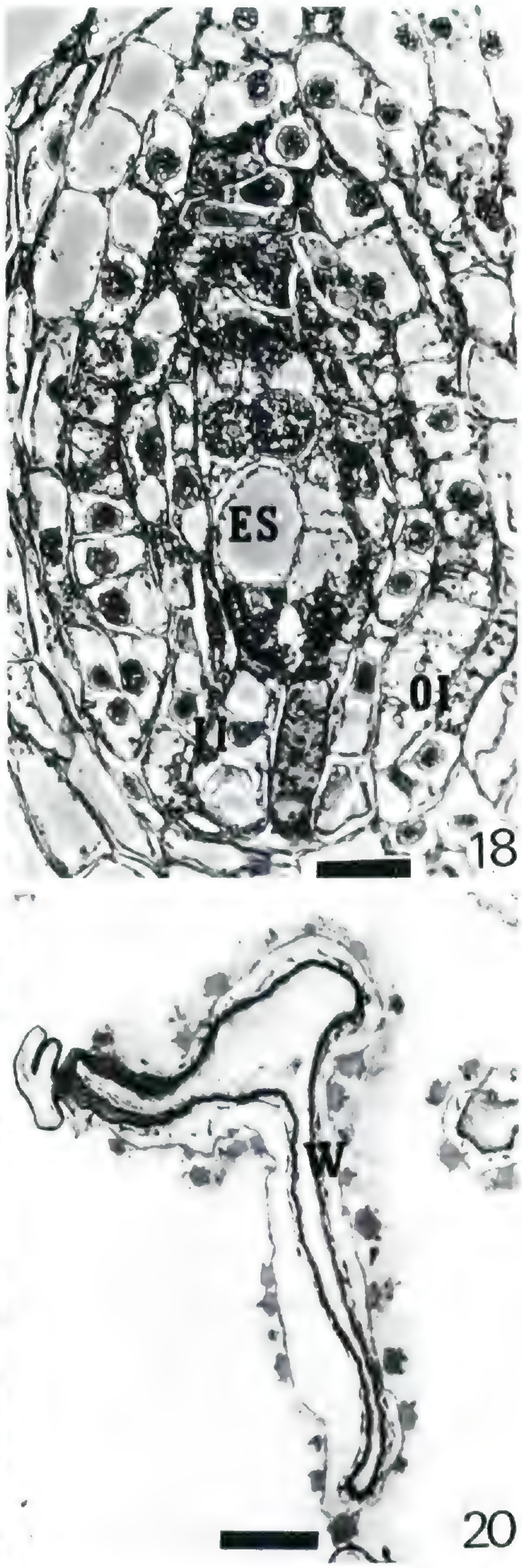
FIGURES 12–16. —12. Longisection of the flower bud, scale bar = 125 μm. 13. Tricellular pollen grains, scale bar = 5.88 μm. 14. Egg apparatus, scale bar = 100 μm.—15. The pollen grains germinate inside the anther, scale bar = 100 μm.—16. Pollen tubes in the base of the anther, scale bar = 23.81 μm. A, anther; B, bract; C, carpels; E, egg; EN, endothecium; II, inner integument; MY, micropyle; PN, polar nuclei; PT, pollen tube; R, receptacle cells; S, synergids; SE, sperm nuclei; TP, tepals; V, vegetative nucleus; W, pollen wall.




FIGURES 17–20. —17. Pollen tubes among receptacle cells, scale bar = 25 μm.—18. The pollen tube enters the micropyle and the embryo sac, scale bar = 62.5 μm.—19. The same picture but greater magnification, scale bar = 25 μm.—20. The walls of an empty pollen grain inside the anther, scale bar = 5.88 μm. ES, embryo sac; II, inner integument; MY, micropyle; OI, outer integument; PT, pollen tube; R, receptacle cells; S, synergids; W, pollen wall.

1986; Martínez & Ramos, 1989; Márquez-Guzmán et al., 1989; Davidse & Martínez, 1990; Rübsamen-Weustenfeld, 1991): anthers bilocular or rarely trilocular or tetralocular, persistent anther epidermis, successive microsporogenesis, tetrads isobilateral, mature pollen grains with three cells.

Maas & Rübsamen (1986) found that the tapetum in Triuridaceae is intermediate between periplasmodial and secretory and tends to protrude into the pollen chamber. The cell walls degenerated at an earlier stage in *Sciaphila* than in *Triuris*. We did not detect a plasmodial stage in the tapetum

of *Lacandonia*, but we did find apparent cytoplasmic bridges among the cells.

There are no data on pollination in Triuridaceae. It is to be expected that several kinds of insects are attracted to the flowers, although this is not directly recorded (Maas & Rübsamen, 1986).

Germination of pollen grains inside the anther sac in *Lacandonia* appears to be unique in Triuridales and a consequence of its cleistogamic reproduction.

Double fertilization in Triuridaceae has not been observed; however, most likely it takes place in several species (Maas & Rübsamen, 1986). Tomlinson (1982) suggested that there is evidence for a possible apomictic process. Dahlgren et al. (1985) mentioned that the egg cell of Triuridales may develop parthenogenetically. Rübsamen-Weustenfeld (1991) observed double fertilization in one embryo sac of *Soridium spruceanum* Miers.

Anderson (1980) described similar pollination and fertilization phenomena to those of *L. schismatica* in four genera of Malpighiaceae. However, these four genera also produce chasmogamous flowers on the same plants. Apparently, in *L. schismatica* all flowers are cleistogamous. In these genera of Malpighiaceae, the cleistogamous flowers generally lack styles, but in *L. schismatica* all the flowers have them.

Philbrick (1984) has found that ovules of two species of *Callitriche* are fertilized by pollen tubes that grow through various tissues between the anther of a male flower and the ovary of an adjacent female flower.

Lord (1981) reported that cleistogamy occurs in 56 families and covers a wide range of dimorphic forms. Under her classification, *L. schismatica* belongs to the category of preanthesis cleistogamy, in which both pollination and fertilization occur in a flower bud which later opens.

Autogamy generally is expected to lead to homozygosity in the population. This has been demonstrated in *L. schismatica* by Coello et al. (1993).

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# LACK OF GENETIC VARIATION IN *LACANDONIA SCHISMATICA* (*LACANDONIACEAE: TRIURIDALES*) IN ITS ONLY KNOWN LOCALITY[1]

*Gerardo Coello,[2] Ana Escalante,[2] and Jorge Soberón[2]*

## ABSTRACT

*Lacandonia schismatica* has only one known population in a small patch of tropical rain forest. Using electrophoretic techniques, we assessed its genetic variation in eight loci; no variation was found. We discuss this result and its implications for the conservation prospects of this threatened species.

*Lacandonia schismatica* (Martínez & Ramos, 1989; Márquez-Guzmán et al., 1989), the only species of Lacandoniaceae, is unique in having a central androecium surrounded by an apocarpous gynoecium. A series of studies of the plant is underway to determine its relationships and taxonomic status, which is still under debate (Stevens, 1991).

The unusual morphology and restricted distribution of *Lacandonia schismatica* suggest that it is an interesting model to study macroevolutionary mechanisms. In this paper we report results on the genetic variation of *L. schismatica* as estimated by enzyme electrophoresis.

## METHODS

The only known locality for *L. schismatica* is the type locality (Fig. 1), which is a ca. 15-ha tropical rainforest patch a few miles north of the Montes Azules Biosphere Reserve in Mexico. The climatological station at Bonampak, close by and at a similar altitude, has a mean annual temperature of 24.6°C and precipitation of 2,609 mm per year (Meave, 1990). The type locality is almost completely surrounded by secondary growth vegetation and cattle pastures. The plants are found within the forest, but only 10–100 m from the edge with a natural savanna. This edge has wet soil, almost a marsh, with an underground water level at about 60 cm below the surface during the dry season. During the dry season, the plants are inconspicuous and can only be found under the litter. During the rains, however, rotting logs are often covered with carpets of *L. schismatica* (E. Martínez, pers. comm.).

Individuals of *L. schismatica* were collected in a 0.5-ha plot (Fig. 1) on three dates, all during the dry season: (A), 10 individuals, April 1988; (B), 72, April 1989; and (C), 27, July 1989. The sample size changed between sites depending on the abundance of the plant. Plants from sample A were collected along a 100-m transect. Plants from samples B and C come from 10–20-$m^2$ high-density patches not more than 50 m away from each other. Live specimens were transported to Mexico City and maintained in growth chambers at 25°C and 80% humidity until prepared for electrophoresis.

Starch gel (12%) enzyme electrophoresis (Vallejos, 1983) was carried out on fresh stem tissue homogenized with gel buffer and absorbed in filter paper wicks (Whatman 17). Eighteen enzymes were assayed, but only eight resolved well in two buffer systems. The enzymes analyzed and the stain references are shown in Table 1.

System I consisted of tris-citrate pH 7 electrode buffer and L-histidine pH 7 gel buffer and system

[1] We thank Esteban Martínez for taking us to the *Lacandonia* site and helping with the fieldwork, and for many discussions about the plant. His assistant Gabriel Aguilar was very helpful as well. Daniel Piñero and Luis Eguiarte made several useful comments on the manuscript. An anonymous referee significantly corrected our English. Gabriela Jiménez drew the location sketch.

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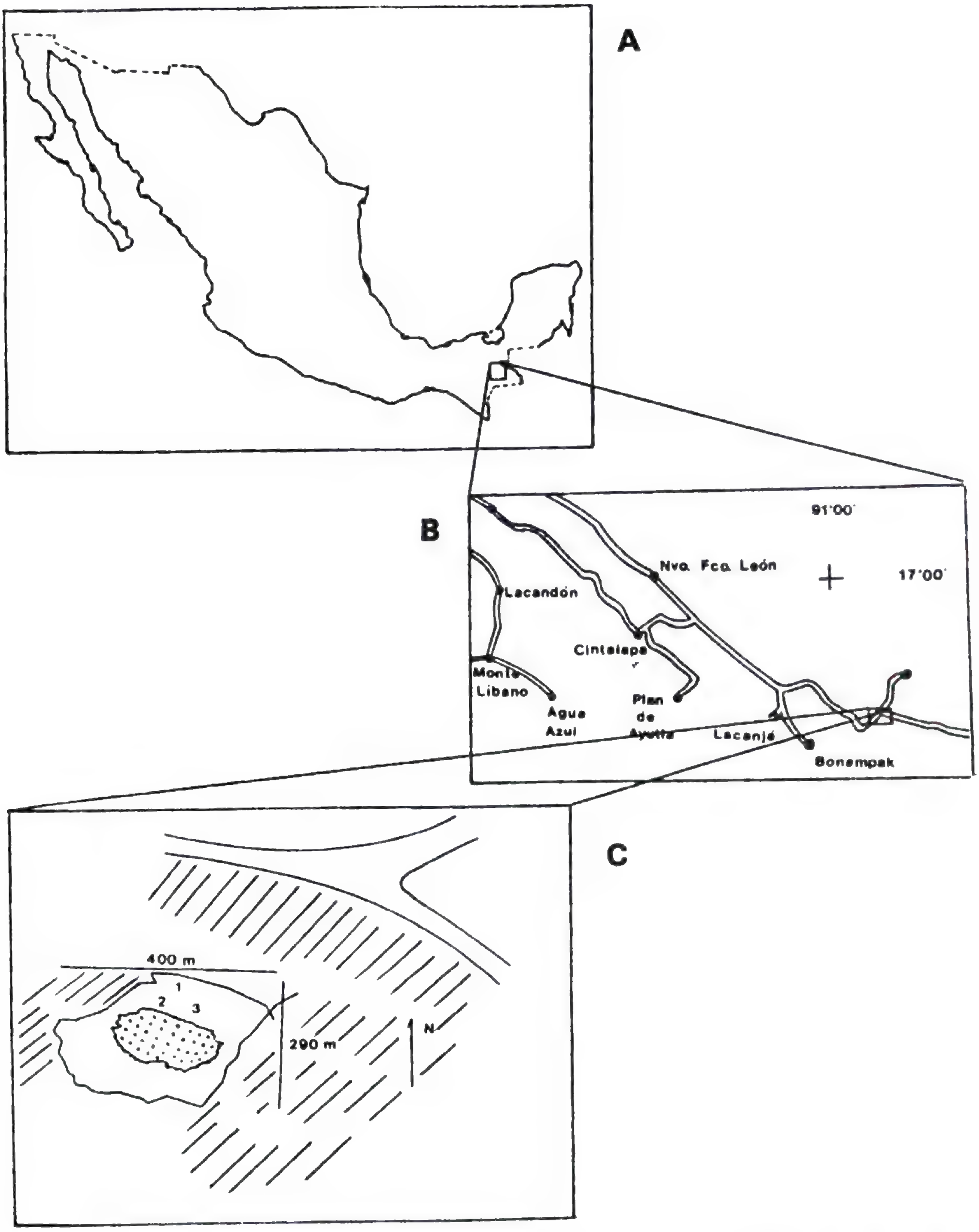


FIGURE 1. Location of the site of *Lacandonia schismatica*. The striped area in C represents cattle pasture land and the dotted area a natural savanna community. Numbers 1, 2, and 3 in C represent collection sites. The polygon around the dotted area is the plot reserved by the Chole Indians to protect the plant.

II of lithium-borate pH 8 electrode buffer and tris-borate pH 8.6 gel buffer (Soltis et al., 1983). Electrophoresis was conducted at 55 mA for system I and 45 mA for system II until the front migrated 10 cm.

## RESULTS

No electrophoretic variation was detected among any of the plants or sites in the 14 loci examined. Stems of 109 individuals were assayed and the

TABLE 1. Enzymes assayed in *Lacandonia schismatica* and stain recipes references.

| Enzyme | Code | Stain reference |
|---|---|---|
| Acid phosphatase (ACP) | E.C. 3.1.3.2 | Soltis et al. (1983) |
| Aconitase (ACO) | E.C. 4.2.1.3 | Wyatt (1989) |
| Alcohol dehydrogenase (ADH) | E.C. 1.1.1.1 | Vallejos (1983) |
| Diaphorase (DIA) | E.C. 1.6.4.3 | Wyatt (1989) |
| Glutamate oxaloacetate transaminase (GOT) | E.C. 2.6.1.1 | Wyatt (1989) |
| Leucine-amino peptidase (LAP) | E.C. 3.4.1.1 | Wyatt (1989) |
| Peroxidase (PER) | E.C. 1.11.1.7 | Vallejos (1983) |
| 6-Phosphogluconate dehydrogenase (6-PGD) | E.C. 1.1.1.44 | Soltis et al. (1983) |

same alleles were expressed in all of them. Table 2 shows the number of loci that resolved for each enzyme analyzed, and the zymogram of Figure 2 shows the activity zone of each loci.

Assuming that the specimens represent a random sample of 218 alleles at each locus, we would have detected any variant allele that existed at an overall frequency of 1.4% or greater with a probability of 95% ($P = 0.986^{218} = 0.05$). Thus, genetic variation is not apparent in our sample.

Lack of genetic variation has also been reported for other endemic species (Hamrick et al., 1979; Waller et al., 1987) and has implications for a conservation program (Holsinger & Gottlieb, 1989).

## DISCUSSION

Lack of genetic variation can be explained by a number of mechanisms, including random drift, genetic bottlenecks (Waller, et al., 1987), and apomixis (Marshall & Brown, 1981). In the case of *Lacandonia schismatica*, the lack of genetic variation can be explained by the autogamic fertilization system reported by Márquez-Guzmán et al. (1993, this issue).

Since *Lacandonia schismatica* is apparently restricted to a small area, the existence of several subpopulations cannot be rejected at this time. The small size of the plant, its location under the litter, and its cleistogamous pollination system (Márquez-Guzmán et al., 1993, this issue) suggest very low levels of gene flow, which may lead to several subpopulations within a small area. The samples used in this study were collected in roughly the same site, and it may be that other subpopulations could have the same low genetic variation but for different sets of alleles. This still has to be tested.

The low genetic variation has contradictory im-

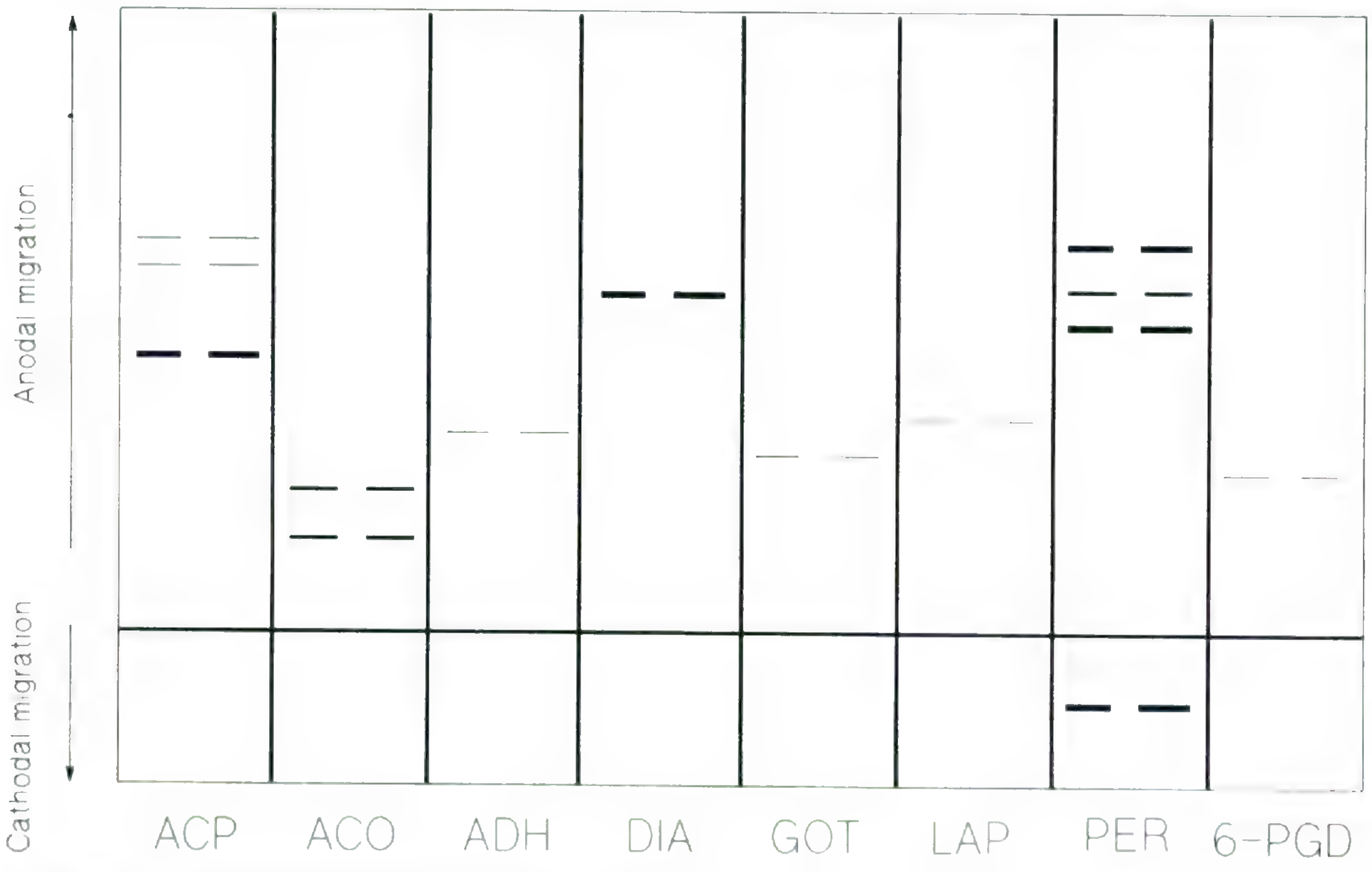


FIGURE 2. Zymogram showing the activity regions for the eight enzymes tested in *Lacandonia schismatica*.

TABLE 2. Enzymes analyzed on each buffer system and the number of loci detected for each one in *Lacandonia schismatica* from Mexico.

| System | Enzyme | Number of loci |
|---|---|---|
| I | ACP | 3 |
| | ACO | 2 |
| | ADH | 1 |
| | PER | 4 |
| | 6-PGD | 1 |
| II | DIA | 1 |
| | GOT | 1 |
| | LAP | 1 |

plications for the conservation of the plant. On one hand, obtaining representative variation for preservation in the greenhouse may be feasible using only a small number of specimens. Unfortunately, to date all attempts to preserve living specimens in growth chambers for more than two or three months have failed. Failure may be due to death of the associated root fungi. On the other hand, the forest patch in which the only known population of *L. schismatica* is located will soon be completely surrounded by secondary vegetation and natural and artificial grasslands. It is likely that microenvironmental conditions in its habitat will change, and it may be the case that *L. schismatica* lacks the genetic variability to adapt to the new situation. Although it now appears that the locality of *L. schismatica* will not be cleared and will be kept as a sanctuary by the owners, the Chole Indian community of Corozal, it is important to begin intensive ecological and genetic studies of the species in order to insure its conservation. It is unlikely that the area in which the plant is located will be able to support a viable population without some degree of management. Given the situation of the habitat, and what is known about the plant's genetics and biology, it is clear that an immediate effort is required to preserve the plant in laboratory conditions and to understand its ecological requirements and genetic structure in order to propose sound management strategies.

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# PATTERNS OF SPECIES DISTRIBUTIONS IN THE DRY SEASONAL FORESTS OF SOUTH AMERICA[1]

*Darién E. Prado[2] and Peter E. Gibbs[3]*

ABSTRACT

Studies of the distributions of species of seasonal woodland habitats in South America by means of dot-mapping and phytosociological analyses indicate the presence of three nodal areas: the Caatingas nucleus of arid northeastern Brazil; the Misiones nucleus, comprising a roughly right-angled triangular area enclosed by lines connecting Corumbá–Puerto Suarez (Brazil/Bolivia) southward to Resistencia–Corrientes in northern Argentina, and eastward to the upper Uruguay River valley system in Argentinian Misiones and Brazilian Santa Catarina, and thus including most of eastern Paraguay and the west bank of the Paraguay River; and the Piedmont nucleus, which extends from Santa Cruz de la Sierra in Boliva to Tucumán and the sierras of east Catamarca in northwestern Argentina. Distribution maps are presented for over 70 taxa that show this kind of distribution pattern or its modifications. Most of the seasonal woodland species of this affinity are notable by their absence from the cerrado vegetation of central Brazil, although some occur on calcareous outcrops in the general cerrados area, and they also avoid the Chaco of northern Argentina. It is proposed that these fragmentary and mostly disjunct distributional patterns are vestiges of a once extensive and largely contiguous seasonal woodland formation, which may have reached its maximum extension during a dry-cool climatic period ca. 18,000–12,000 BP, coinciding with the contraction of the humid forest.

Various authors have drawn attention to the "savanna corridor" (Schmidt & Inger, 1951) or "diagonal of open formations" (Vanzolini, 1963, 1974), which extends across South America from Maranhão–Ceará in north-northeastern Brazil, to the Chaco region of northern Argentina (Fig. 1), and numerous commentaries on possible floristic and faunistic links have been made (e.g., Andrade-Lima, 1954, 1982; Vanzolini, 1974; Prance & Schaller, 1982; Bucher, 1982; Haffer, 1985; Ratter et al., 1988), particularly for the Caatinga–Chaco poles of this diagonal. In the course of a recent critical reevaluation of the alleged floristic links between the caatingas of northeastern Brazil and the Gran Chaco vegetation of northern Argentina–Paraguay–Bolivia (Prado, 1991), a series of dot-map distributions were plotted for woody species of the deciduous and semideciduous forests of South America. The Caatinga–Chaco links proved to be negligible, but a different and rather more interesting distribution pattern emerged.

The distributions hint at a once extensive arc of seasonal woodland, which ranged from northeastern Brazil (with some Amazonian and Caribbean links) through southeastern Brazil to the confluence of the Paraguay and Paraná rivers, into southwestern Bolivia and northwestern Argentina, and extending sporadically northward in dry Andean valleys of Peru. In most cases, these species skirt the impoverished soils of the central Brazilian cerrado vegetation (Eiten, 1972), but some taxa "island-hop" across this area by way of the restricted outcrops of calcareous-rich soils within the cerrados.

## CLIMATIC CHANGES IN SOUTH AMERICA DURING THE LAST GLACIAL MAXIMUM

Many authors (e.g., Damuth & Fairbridge, 1970; Ab'Sáber, 1977, 1982) have postulated a major dry-cool climatic period in South America at the time of the Northern Hemisphere Wisconsin–Würm

[1] We thank the directors of the Royal Botanic Gardens at Edinburgh and Kew for provision of herbarium and library facilities during repeated visits, and also to the following herbaria for the loan of specimens: Arnold Arboretum of Harvard University, Conservatoire et Jardin botaniques de la Ville de Genève, Gray Herbarium of Harvard University, Empresa Pernambucana de Pesquisa Agropecuária, Recife, and Herbário, Botánica y Ecología Vegetal, Universidad de Rosario. D. Prado is grateful to Maria Angêlica Figueiredo, Maria das Graças, M. Pires, and Arnildo and Vali Pott for kind assistance with field excursions in Brazil, and acknowledges financial assistance from CONICET Argentina, the University of St. Andrews, and the Committee of Vice-Chancellors and Principals of the Universities of the U.K. for an Overseas Research Student's award.

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glaciation, about 18,000–12,000 BP. There has been considerable discussion devoted to the consequences of such a dry period with regard to the contraction of the humid forest to isolated "islands" and the "refuge theory" as a possible stimulus for speciation events that are reflected in present-day Amazonian forest diversity patterns (Brown & Ab'Sáber, 1979; Prance, 1973, 1982, and various contributions in Prance, 1982). Other authors, however, have urged caution in interpreting present-day species distributional patterns in terms of supposed Pleistocene forest refuges (e.g., Benson, 1982; Nelson et al., 1990).

Unfortunately, paleo-palynological studies for South America, which could provide valuable evidence for dry periods and consequent vegetational changes, are sparse and mostly apply to Andean areas (e.g., Van der Hammen, 1974, 1982), and the few studies in the Amazonian regions are for more recent Holocene strata (Absy, 1982). However, on the basis of local palynological investigations some authors have attempted to circumscribe in more detail the possible regional shifts in climate and vegetation in the Paleocene (Markgraf, 1989), while others have reported evidence that conflicts with areas of alleged humid forest refuges (Kam-biu & Colinvaux, 1985; Colinvaux, 1989).

Most discussion concerning the postulated Pleistocene dry periods in South America has focused on the consequences of contraction of the humid forest, and less attention has been given to the influence of such climatic changes on the expansion of semideciduous and deciduous vegetation of the region. Here we present a series of distribution maps for a number of species of seasonal woodland formations, which reveal floristic links between the flora of the caatingas vegetation of semiarid northeastern Brazil (sensu Andrade-Lima, 1981) and two other areas. In our opinion, these distributions are remnants of once continuous forests, and they provide some evidence for the previous extensive occurrence of seasonal forests in South America. While we are fully conscious of the dangers of facile interpretations from dot-maps, and particularly the possible influence of localized collecting, we consider that the repetitive distributions that emerge from these maps do reflect past floristic links. We offer these distribution maps as a contribution to the ongoing debate concerning the historical biogeography of the seasonal formations in South America.

FIGURE 1. The "dry diagonal" of seasonal woodlands in South America with Caatingas, Cerrado, and Chaco areas delimited.

## METHODS

This series of species distribution maps began as an attempt to plot accurately the full distributions of the woody taxa of the caatinga vegetation (Andrade-Lima, 1981; Prado, 1991) of northeastern Brazil. It soon became evident that many of the nonendemic caatinga species showed a common overall distribution pattern that mostly avoided the cerrado region but extended to southeastern and southern Brazil and, in many cases, into well-defined areas in Paraguay, Argentina, and Bolivia. The maps involved an exhaustive check of the taxonomic literature and verification of the identity of species cited in diverse floristic lists, made possible by repeated visits to The Royal Botanic Gardens at Edinburgh and Kew, and herbarium material obtained on loan from various institutions. The species dot-maps are based on verified specimens or citations in modern taxonomic revisions (solid symbols) together with citations in reliable vegetation surveys in the areas concerned (open symbols).

In addition to mapping species distributions, a suite of floristic lists from 18 seasonal woodland communities across South America were compared by means of a classic phytosociological analysis of the Zurich-Montpellier school, in the version modified by Mueller-Dombois & Ellenberg (1974), and also by means of a complete linkage algorithm from Wishart's (1987) package employing Sørensen's (1948) similarity index, and a Principal Compo-

nents Analysis from the JMP IN statistical software (Prado, 1991). Details of these latter analyses are not given here, but both approaches strongly supported the close floristic links between the caatinga vegetation and woodlands in south-southeastern Brazil and Paraguay, and the piedmont forests of northwestern Argentina–southern Bolivia.

### Residual Pleistocenic Seasonal Formations Arc

Ab'Sáber (1977) has postulated that during a major dry episode in South America, equivalent to the Wisconsin–Würm glacial period, there was an expansion of semiarid vegetation in the continent. According to this view, caatinga-like vegetation, which usually occurs on mineral-rich soils, may well have surrounded a core area of cerrado vegetation in central Brazil, and both seasonal formations very probably extended into the Amazon region, whereas tropical rainforests underwent contraction. It is likely that the slow return of a more humid climate during the past 12,000 years, in addition to favoring a re-expansion of the evergreen forest, was also accompanied by leaching and acidification of soils in various areas, perhaps increasing the cerrado region, and fragmenting the originally much more widespread semiarid vegetation of base-rich soils (Ratter et al., 1988).

A number of the woody species that are likely to have been involved in the cyclic expansion-retreat migrations of the Pleistocene are today members of diverse tropical and subtropical deciduous forest communities in South America, such as the caatingas of northeastern Brazil and some semideciduous (i.e., non-Mata Atlântica) forests in São Paulo and Paraná states, the forests of the upper Uruguay River valley and most of those surrounding the Paraguay–Paraná rivers system, the serranías of Santiago and Chiquitos in southeastern Bolivia, the piedmont forests in the so-called Transitional areas in northwestern Argentina and southwestern Bolivia (running parallel to the sub-Andean mountains from Tucumán in Argentina to Santa Cruz de la Sierra in Bolivia), and more scattered outposts in semiarid and arid Andean valleys in northern Bolivia, throughout Peru and sometimes even reaching southwestern Ecuador. Some of these species are not only important members of these communities but are also dominant in several instances.

One such case, and here taken as paradigm, is that of the mimosoid *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altschul ("angico," "cebil"). For the distribution of this species (Fig. 2A) three nuclei can be identified. The first and major nucleus consists of the caatingas of northeastern Brazil, where the "angico" is a very important and frequent tree, and it is present in most of Andrade-Lima's (1981) vegetation units. Outside the caatingas, it has been reported in the "brejos" from Pernambuco (Andrade-Lima, 1964), particularly in the dry forests of the slopes of the "serras," and in the so-called "caatingas" in Maranhão state (Galvão, 1955). Bigarella et al. (1975) claimed that disjunctions of caatingas occur on the road Coroatá–Vargem Grande (Maranhão), and the exsiccatum marked on our map corresponds to Presidente Dutra, which is just to the south of these localities. This northeastern Brazilian nucleus for the angico type of distribution (which we can call the Caatingas nucleus) is intermittently linked to the second nucleus, which occurs along the Paraguay–Paraná rivers system, by the way of mesotrophic cerradão woodlands in Goiás and Mato Grosso (Ratter et al., 1978), and in Mato Grosso do Sul (Ratter et al., 1988; Prado et al., 1992).

The second nucleus has a somewhat triangular shape with its northernmost apex on the axis Puerto Suárez–Corumbá (Bolivian–Brazilian border), a straight meridian side reaching south on the axis Resistencia–Corrientes in Argentina and thus paralleling the Paraguay River up to its confluence with the Paraná River, a latitudinal side eastward from that confluence to the upper Uruguay River valley in Misiones (Argentina) and Santa Catarina (Brazil), and from here a diagonal side returning in northwest direction to Pto. Suárez–Corumbá. Thus, this nucleus (which we can refer to as the Misiones nucleus, employing this term in its older, more general geographical concept rather than the current restricted Argentinian or Paraguayan usage) includes nearly all of eastern Paraguay and a good deal of the western bank of the River Paraguay, that is, a north–south strip parallel to the river and several kilometers inland in the geographical Gran Chaco region. Within this triangle, *Anadenanthera colubrina* var. *cebil* is common but rarely dominant. It has been reported by Fiebrig (1933) along the western bank of the River Paraguay, by Tortorelli (1967) and Esser (1982) for several areas of eastern Paraguay, by Morello & Adámoli (1967) for eastern Formosa, and by Eskuche (1986) for northeastern Argentina in the Paranense phytogeographical province (Cabrera & Willink, 1980).

This second nucleus connects with the third one, located in southwestern Bolivia and northwestern Argentina, via the Santiago and Chiquitos hill ranges, forming a curved line uniting Corumbá to Santa

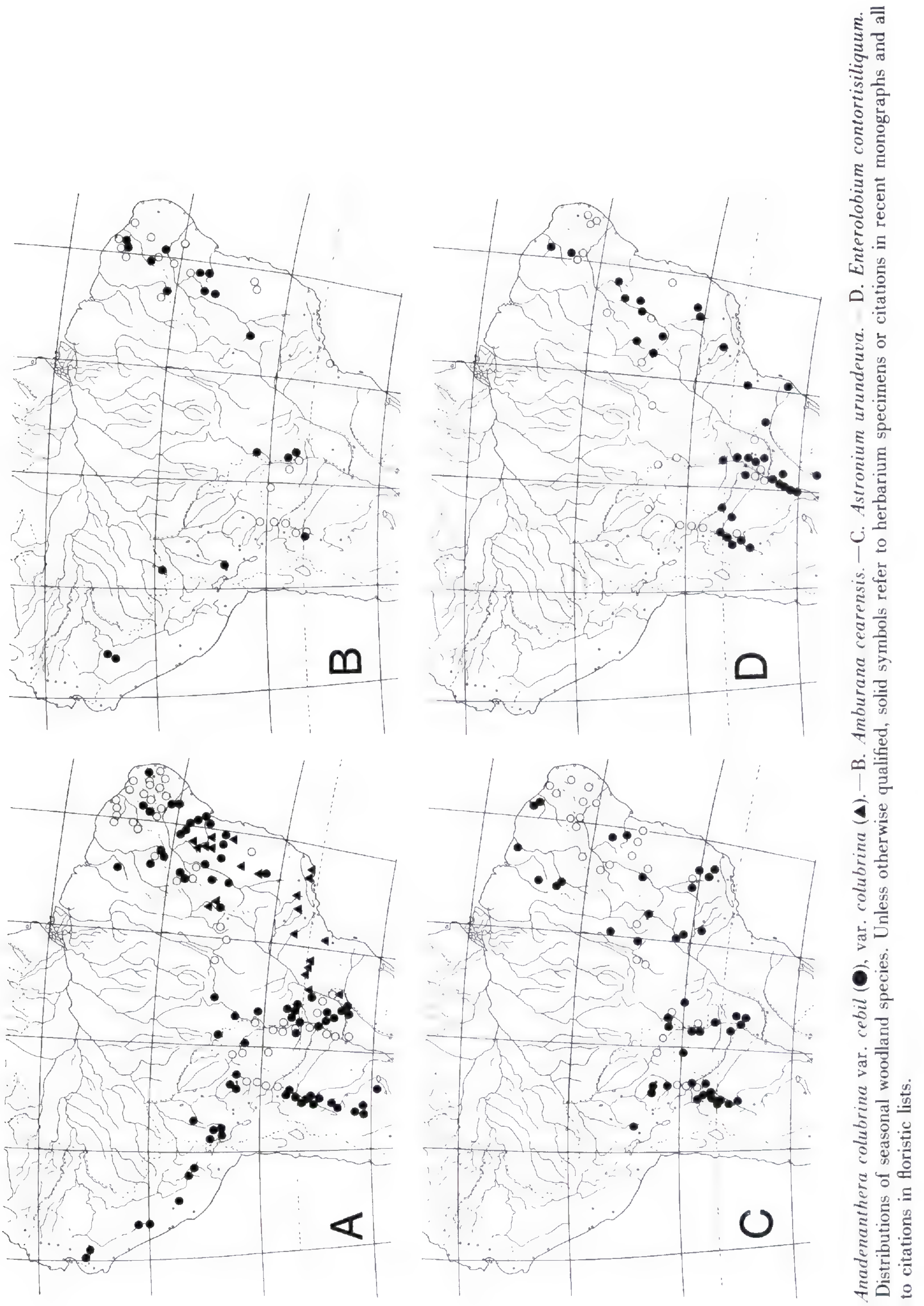


FIGURE 2[4].—A. *Anadenanthera colubrina* var. *cebil* (●), var. *colubrina* (▲).—B. *Amburana cearensis*.—C. *Astronium urundeuva*.—D. *Enterolobium contortisiliquum*. [4] FIGURES 2–15. Distributions of seasonal woodland species. Unless otherwise qualified, solid symbols refer to herbarium specimens or citations in recent monographs and all open symbols refer to citations in floristic lists.

Cruz de la Sierra. The flora of this region has scarcely been studied and even less collected, but Herzog (1910, 1912) gave a fairly accurate impression of what the vegetation was like in the area. In the sector enclosed by this previous line and hills, by the western limit of the second nucleus, and by the north–south narrow strip of the third nucleus, the true chaco vegetation is encased. There are very few outposts of *Anadenanthera colubrina* var. *cebil* within the Chaco area (as is the case with most of the species with this pattern of distribution). The Cerro León records of this tree are not an exception to its absence from the plains of the Chaco sens. str., because the vegetation on the slopes of this tectonic horst (which comprises Silurian and Devonian rocks as opposed to the æolian sediments surrounding the hill) shows strong links with the sub-Andean Piedmont forests in northwestern Argentina (Ramella & Spichiger, 1989, *sub* Transitional Forests).

The third nucleus extends from Santa Cruz de la Sierra south to Tucumán and the sierras of eastern Catamarca in Argentina. This follows the piedmont area of the sub-Andean Mountains, which is the area of the so-called transitional forests, so-named because their floristic composition has been considered to be intermediate between that of the chaco thorn forests and the upland subtropical rainforests (the "Yungas" sens. str.). We can refer to this nucleus, therefore, as the Sub-Andean Piedmont nucleus. *Anadenanthera colubrina* var. *cebil* was so important in the southern half of this nucleus in Argentina that Lillo (1919, as cited in Hauman, 1931, and Digilio & Legname, 1966) called it "zona del cebil," but today there is little left of the original vegetation in this area, which is known locally as "tipa-pacará" forest (from the species *Tipuana tipu* (Benth.) O.Kuntze and *Enterolobium contortisiliquum* (Vell.) Morong). The northern remainder of the nucleus where the angico occurs comprises the "palo blanco" forest, dominated by *Calycophyllum multiflorum* Griseb. and *Phyllostylon rhamnoides* (Poisson) Taubert, and which extends from mid-eastern Jujuy in Argentina to, presumably, Santa Cruz de la Sierra. *Anadenanthera colubrina* var. *cebil* is one of the five commonest members of both these forests (Cabrera, 1976: 7).

From this third nucleus this species, and the pattern of distribution dealt with here, becomes scattered along the northeast-facing slope of the Andes in Bolivia and southern Peru, i.e., from Santa Cruz to Cuzco, to even more scattered localities in dry inter-Andean valleys such as those of the Apurímac, Huállaga, and Marañón rivers (Weberbauer, 1936), finally reaching southern Ecuador in what corresponds to the "Savannah and Dry Scrub vegetational types" (see map in Harling, 1979). The distribution of the typical variety, *Anadenanthera colubrina* var. *colubrina*, further extends the range of the species (Fig. 2A), since although it occurs sympatrically with variety *cebil* in the southern area of the caatingas in Bahia, and also in Misiones in Argentina, it is distributed allopatrically in Rio de Janeiro state and the planalto forests of São Paulo and Paraná states. Altschul (1964) has argued cogently that the typical variety evolved from variety *cebil*, in which case variety *colubrina* has developed in wetter areas than those of its parental stock.

A number of woody caatinga species have a similar, sometimes virtually identical, distribution pattern to that of *Anadenanthera colubrina*. For example, *Amburana cearensis* (Allemão) A. C. Smith (Leguminosae) is a frequent, albeit not abundant, characteristic tree of the caatingas even in the more shrubby types of communities, and it occupies a similar niche in the palo blanco forest (Piedmont nucleus), while it is rather rare in the Misiones nucleus except for some dense populations on calcareous substrate on the Apa River region in Paraguay (Fiebrig, 1933; Tortorelli, 1967). It has also been reported for the Cerro León (Ramella & Spichiger, 1989), and it appears very occasionally in the Andean sector of this pattern of distribution; a collection from Acre state in Brazil should be noted (Fig. 2B). The tree *Astronium urundeuva* (Allemão) Engl. (Anacardiaceae) is an important member of the arboreal caatinga, in which it is characteristic and dominant (Andrade-Lima, 1981), but it also extends into the shrubby caatinga as an isolated low tree (as does *Amburana cearensis*, according to Egler, 1951). *Astronium urundeuva* is considered an indicator species of mesotrophic facies cerradão (cerradão is a well-developed woodland type, which is usually characteristic of richer soils) within the cerrado area in central Brazil (Ratter et al., 1978). It has also been collected in the Cerro León, and it is very frequent in the sub-Andean Piedmont nucleus, but there are no records from the Andean dry valleys (Fig. 2C).

The mimosoid tree *Enterolobium contortisiliquum* (Vell.) Morong is usually conspicuous, not for its frequency but rather for its size. Somewhat scarce in the caatingas (Fig. 2D), it has been reported for the agreste (Andrade-Lima, 1954) and arboreal caatinga (Andrade-Lima, 1975). In the forests of southeastern Brazil its presence is recorded by collections and phytosociological works (Martins, 1979), and it is an important component

of the vegetation on the banks of the Paraguay–Paraná system (Reboratti & Neiff, 1986; Prado et al., 1989), and also of the sub-Andean piedmont forests (particularly in the tipa-pacará variant), but again is absent from the Andean area. *Enterolobium contortisiliquum* has also been collected in the gallery forests that border the Chaco vegetation (see Fig. 2D and Morello & Adámoli, 1974), where it occurs with other nonchaquenian subtropical species, on the alluvial levees beside the main rivers (Adámoli et al., 1972). *Pterogyne nitens* Tulasne (Leguminosae) has a very similar distribution (Fig. 3A) and is also reported for gallery forest and humidity-dependent communities within the Chaco (Morello, 1967; Morello & Adámoli, 1974), but as a rather rare element of the latter. The species *Ruprechtia laxiflora* Meisn. (Polygonaceae) was originally described by Meisner (1855) from Blanchet exsiccata collected in the caatingas (Cocucci, 1961), but it was not recorded subsequently in this area until recent collections by Harley et al. from around Camaleão in Bahia. It was, however, abundantly collected in Paraguay and Argentina in both the Misiones and Piedmont nuclei, where it is a very important element (Fig. 3B). The scandent shrub or treelet *Celtis pubescens* (Kunth) Sprengel (Ulmaceae) follows much more closely the *Anadenanthera colubrina* var. *cebil* pattern (although it is far less frequent in the caatingas), and it reaches central Ecuador (Fig. 3C) and is also recorded from Acre state in Brazil.

One of the most important and characteristic trees in the caatingas is *Schinopsis brasiliensis* Engler (Anacardiaceae). Engler (1876) recognized two varieties, variety *glabra* Engler and the typical variety of this species. Meyer & Barkley (1973) subsequently considered the former variety to merit specific status, based on its lack of indumentum and larger leaflets when compared to variety *brasiliensis*. However, from the numerous exsiccata we have examined it would seem that although presence–absence of indumentum is a fairly consistent character, leaflet size is unreliable. A traditional view has been taken of *S. brasiliensis*, therefore, to include the two sympatric varieties, *brasiliensis* and *glabra*, and they have been mapped together (Fig. 3D). This tree is not only present and abundant in the caatingas, from where it extends into isolated localities in the Federal District of Brazil and in Minas Gerais (where it has been reported to form a dense community in a flood-prone area by Pinto, 1985), but it is also the dominant species in forests in Mato Grosso do Sul (Prado et al., 1992). *Schinopsis brasiliensis* also extends from Corumbá to the west along the Santiago and Chiquitos ranges (Herzog, 1910), and there are many exsiccata from the humid slopes of the Andes in northwestern Bolivia, but it has not been recorded for Peru, where, however, it seems to be replaced by a similar and little known species, *S. peruviana* Engler, which has been collected only twice (Fig. 3D).

The species *Piptadenia viridiflora* (Kunth) Benth. (Leguminosae) poses an interesting case since it is an important element of the caatingas, frequently reported in the literature, whereas it is a relatively rare species in northwestern Argentina in the piedmont deciduous forests (Fig. 4A). Burkart (1952) cited this tree for Colombia and Venezuela (presumably for the dry Caribbean area), but no exsiccata or references have been encountered to confirm this assertion. Both the species and the genus seem to be missing from the Misiones nucleus of this pattern of distribution, that is, the Paraguay–Paraná system, but this may simply be due to a problem of taxonomic interpretation, since all previously considered *Piptadenia* species for this area have been transferred to other genera (*Anadenanthera* Speg., *Goldmania* Rose ex Micheli, *Parapiptadenia* Brenan). It is noteworthy that the species *Goldmania paraguensis* (Benth.) Brenan, endemic to this sector, is very close to section *Pityrocarpa*, to which Burkart (1952) referred *Piptadenia paraguensis* (Benth.) Lindm. (= *Goldmania paraguensis*), while Brenan (1955) transferred *Piptadenia viridiflora* to his genus *Pityrocarpa*.

There is only one collection of *Carica quercifolia* (A. St.-Hil.) Hieron. (Cariacaceae) known from the caatingas, from Irecê in Bahia (Badillo, 1971), and this would represent a very wide disjunct occurrence from the main, "amphi-Chaco," area of distribution of this species (Fig. 4B) if it were not for three additional isolated collections in Goiás, Minas Gerais, and São Paulo states, which tenuously link the Bahian record to the second nucleus of the Pleistocenic Arc. The rest of the distribution is divided into two more or less continuous zones separated by the Chaco plains. One corresponds to the Misiones nucleus, extending eastward along the upper Uruguay basin to include the planalto forests, but also with an extension westward into the eastern Chaco. The second corresponds to the piedmont deciduous forests on the sub-Andean slopes. *Carica quercifolia* is also common in dry valleys between Andean ranges in northwestern Bolivia and southern Peru.

The shrub *Combretum leprosum* Mart. (Combretaceae) is another typical caatinga species that follows relatively well the Pleistocenic Arc (Fig.

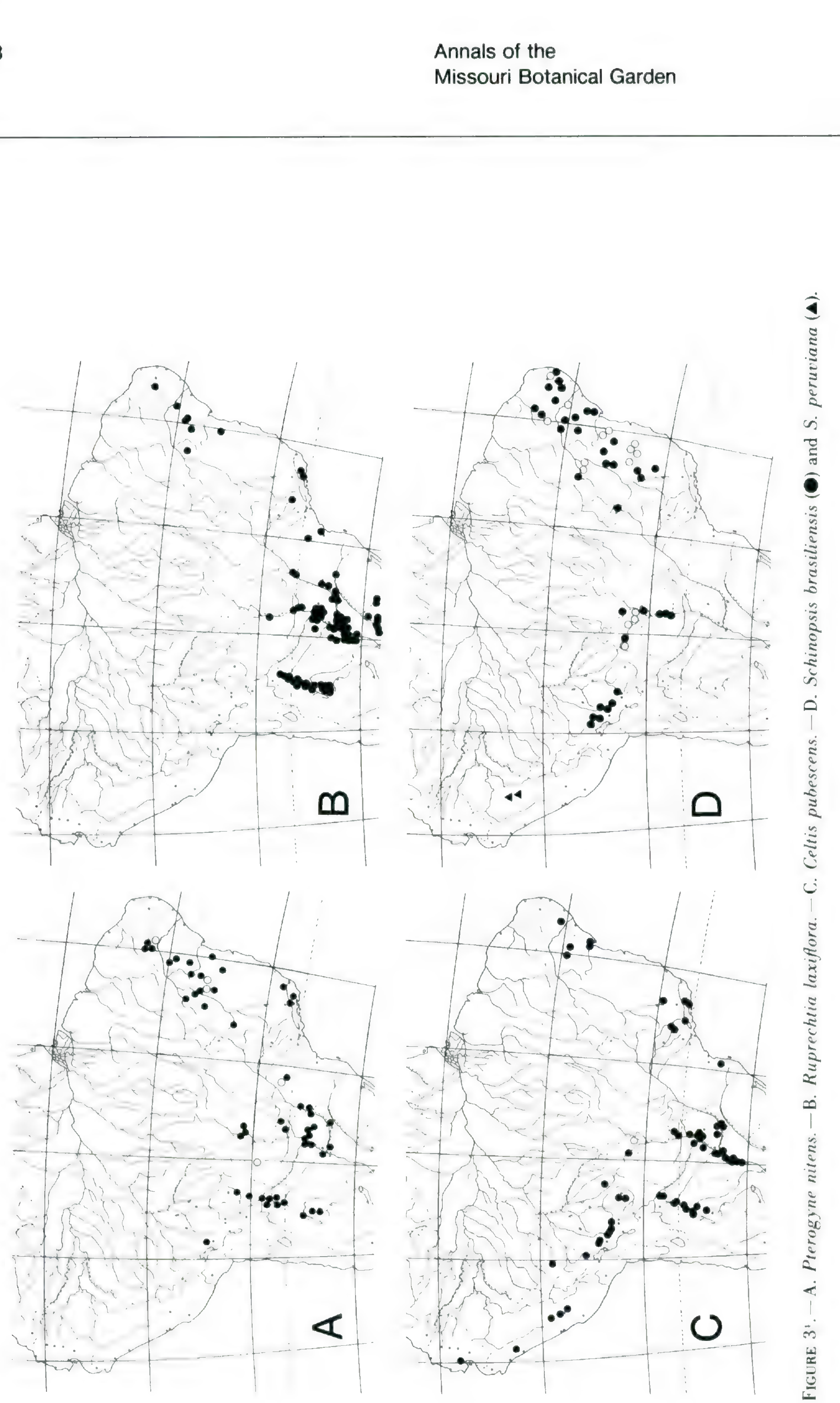


FIGURE 3[1].—A. *Pterogyne nitens*.—B. *Ruprechtia laxiflora*.—C. *Celtis pubescens*.—D. *Schinopsis brasiliensis* (●) and *S. peruviana* (▲).

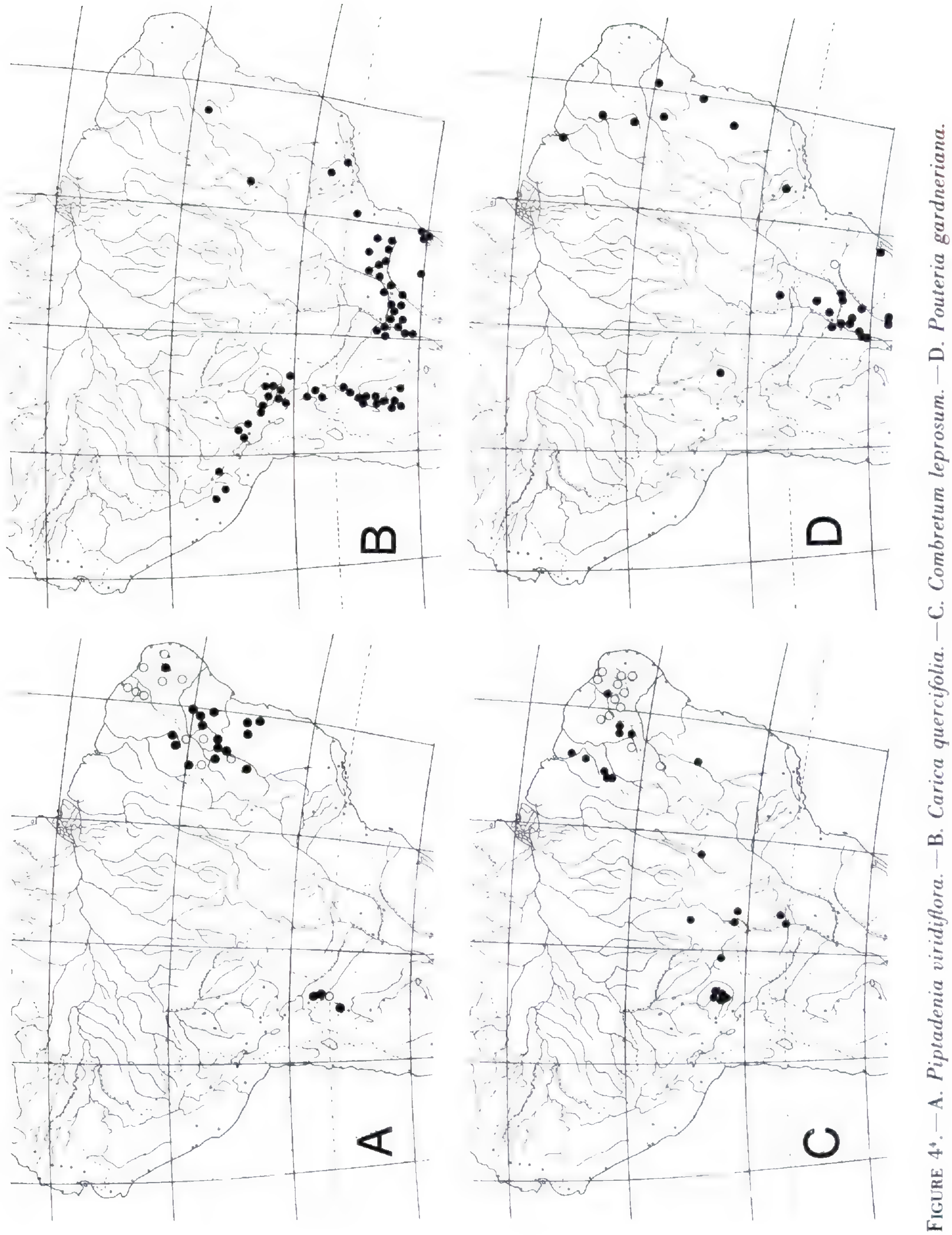


FIGURE 4*.—A. *Piptadenia viridiflora.* —B. *Carica quercifolia.* —C. *Combretum leprosum.* —D. *Pouteria gardneriana.*

4C). It is also common in Maranhão state in areas suspected of having links with the caatingas, and it has been collected in the River Paraguay valley and in Santa Cruz de la Sierra area, but seems to be missing from there to the south and northwest. The pattern followed by *Pouteria gardneriana* (D. C.) Radlk. (Sapotaceae) is somewhat more uncertain, since although it is well recorded in the caatingas and in the Paraguay–Paraná system, it is unclear whether it spreads into the Piedmont nucleus apart from one collection in Santa Cruz in Bolivia (Fig. 4D).

*Sterculia striata* A. St.-Hil. & Naudin (Sterculiaceae) is a rather different case (Fig. 5A), since it only marginally appears in tall, arboreal caatinga (Andrade-Lima, 1975; Ratter et al., 1978). It is much commoner in mesophilous forests within the cerrados expanse or in mesotrophic cerradão (Ratter et al., 1978, 1988), but it shuns the poor soils of the cerrado sens. str. It extends into the Amazon valley (Taroda, 1984) as well as to the River Paraguay area, particularly on calcium-rich soils (Ratter et al., 1988; Prado et al., 1992), and its westernmost collections come from the area of Santa Cruz.

The small bignoniaceous tree *Tabebuia caraiba* (Mart.) Burch. (synonymized with *T. aurea* (Manso) Benth. & Hook. in Gentry, 1992) has an unusual distribution in that it is common in the cerrados on typically poor-quality soils, but is also relatively common in the caatingas of Pernambuco (Andrade-Lima, 1954, 1960) and Bahia, and it can be found in the Amazon valley around Santarem. This species has also been frequently collected in the Paraguay River valley sector from Brazil to Argentina, while Ramella & Spichiger (1989) reported it for cerrado-like communities on top of the plateau in Cerro León. *Tabebuia caraiba* also appears occasionally in central Bolivia, including a specimen collected near Santa Cruz de la Sierra, thus conforming somewhat to the Pleistocenic Arc (Fig. 5B), although the main core area of this species is the central Brazilian cerrado area. Somewhat similar distributions, with extensive occurrence in typical cerrado, are shown by *Hymenaea martiana* Hayne (Leguminosae) and *Machaerium acutifolium* J. Vogel (Leguminosae) but both species lack the Amazonian extension (Fig. 5C, D). *Hymenaea martiana* spreads from the caatinga into the cerrado savannas in Goiás, the Federal District, and Minas Gerais, as well as occurring in the forests in the Paraguay River area. *Machaerium acutifolium* also occurs in the cerrados as well as the caatingas, and extends south into the Mata Atlântica in Rio de Janeiro, isolated "campo" areas in Minas Gerais and São Paulo, and in forests in eastern Paraguay. This latter species has a somewhat invasive–pioneer tendency, which may account for its more extended distribution.

A number of genera show vicariad species that occupy parts of the Pleistocenic Arc. One such case is *Brunfelsia* L. (Solanaceae). Recently, Plowman (1979) drew attention to the fact that *B. uniflora* (Pohl) D. Don forms a link between the older Andean species and the eastern Brazilian ones within section *Franciscea*. It has been collected in northern Venezuela, in Roraima (Brazil) and neighboring Guyana, also in the Yungas area of the eastern-facing slopes of the Andes in southwestern Bolivia and northwestern Argentina, to then reappear sporadically in the caatingas and more abundantly in the Atlantic forests and planalto forests in eastern Brazil. Two additional species, *B. pilosa* Plowman and *B. australis* Benth., are apparently derived from *B. uniflora*. *Brunfelsia australis*, previously treated as a subspecies of *B. uniflora*, fills in the southernmost gap corresponding to the Misiones nucleus in the distribution of its mother species in Paraguay and northeastern Argentina (Fig. 6A). *Brunfelsia uniflora* thus shows a similar but much more complete distribution pattern (Fig. 6B) to that of *Commiphora leptophloeos* (Mart.) Gillet (Burseraceae).

The genus *Patagonula* L. (Boraginaceae) seems to be endemic to the Pleistocenic Arc (Fig. 6C). This genus comprises only two species: *P. bahiensis* Moricand is endemic to the caatingas, whereas the type species, *P. americana* L., has been collected or reported for the forests in Paraná state in Brazil, the upper Uruguay River basin (Klein, 1972), eastern Paraguay, and northeastern Argentina in subtropical forests from Misiones to the eastern Chaco district (Cabrera, 1976; Lewis & Pire, 1981). It is also the third most important species in the Piedmont nucleus forests of northwestern Argentina and southern Boliva (Cabrera, 1976). Although *Patagonula* has not been reported from other areas of the Pleistocenic Arc, it would not be surprising for it to be encountered in the future in the rather poorly studied areas of Cerro León, the Santiago and Chiquitos ranges, or south of Santa Cruz de la Sierra.

The genus *Loxopterigium* Hook. f. (Anacardiaceae) presents five disjunct species in South America (Fig. 6D). The scarcely known *L. gutierrezii* Barkley was collected only once in the Caribbean sector of Colombia, while *L. sagotii* Hook. f. is better known from the Guianas. The tree *L. hu-*

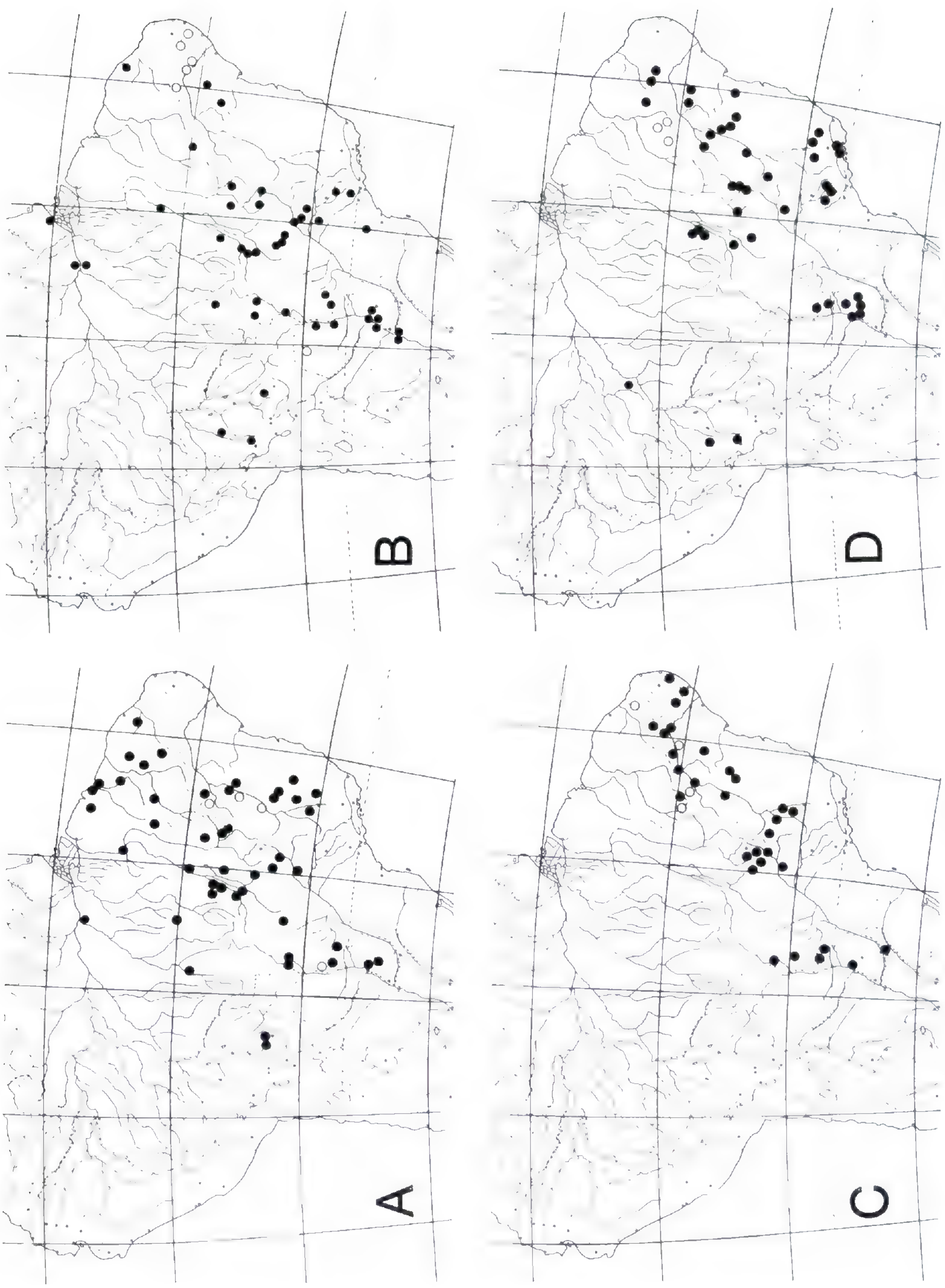


FIGURE 5[1]. —A. *Sterculia striata*. — B. *Tabebuia caraiba*. —C. *Hymenaea martiana*. —D. *Machaerium acutifolium*.

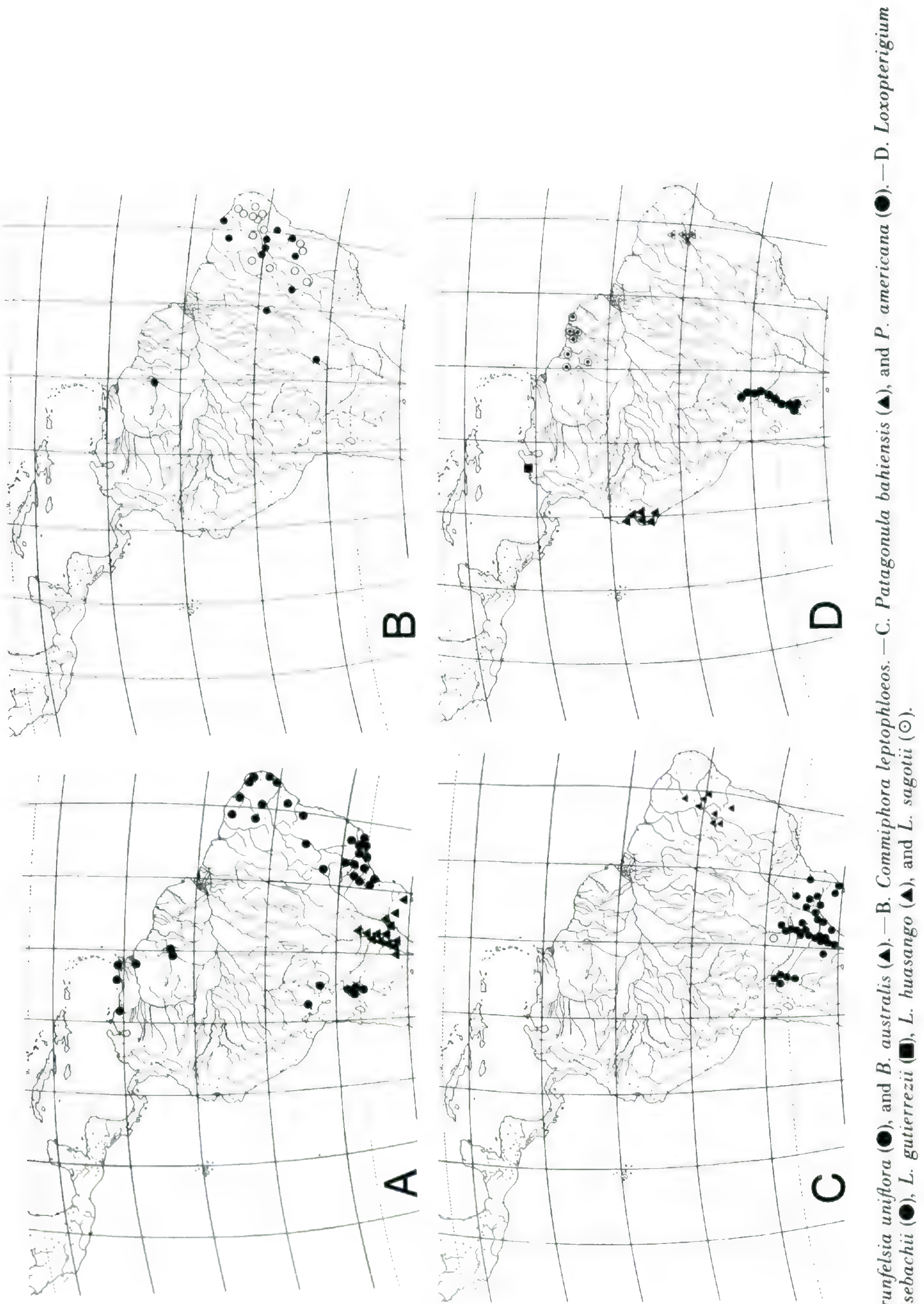


FIGURE 6[4].—A. *Brunfelsia uniflora* (●), and *B. australis* (▲).—B. *Commiphora leptophloeos*.—C. *Patagonula bahiensis* (▲), and *P. americana* (●).—D. *Loxopterigium gardnerii* (△), *L. grisebachii* (●), *L. gutierrezii* (■), *L. huasango* (▲), and *L. sagotii* (⊙).

*asango* Spruce appears only in seasonal semiarid to arid formations in coastal southwestern Ecuador and northern Peru, while the caatinga woodlands of a small area of Piauí and Bahia contain the few recorded populations of *L. gardneri* Engl. (= *Apterokarpos gardneri* (Engl.) Rizzini). Finally, *L. grisebachii* Hieron. & Lorentz ex Griseb. is an important member of the sub-Andean piedmont forests in northwestern Argentina and southern Bolivia, which separates chaco vegetation from the rain and cloud forests of the Yungas. In this case, therefore, the allopatric species within a small genus together comprise the familiar distribution pattern of this Seasonal Forests Arc in South America.

The unresolved taxonomic problem (see comments in Burkart, 1949, and Lewis, 1987) of the *Geoffroea striata* (Willd.) Morong–*G. spinosa* Jacq. (Leguminosae) complex provides another example of the Seasonal Forests Arc (Fig. 7A). In our experience, the diagnostic characters provided by Burkart (1949) fail to separate these alleged species clearly, and this complex is treated here as one polymorphic unit which, however, segregates well from the only other species of the genus, the typically but not exclusively chaquenian *G. decorticans* (Hook. & Arn.) Burkart. The *G. striata–spinosa* complex appears in northern Venezuela, western Ecuador and adjoining Peru, and in central Bolivia in the Yungas-like area of the Río Grande or Piraí, for the Andean related part, whereas in the lowlands there are essentially two nuclei: the Caatingas and Misiones. A similar pattern is followed by *Ipomoea carnea* Jacq. subsp. *fistulosa* (Mart. ex Choisy) Austin (Convolvulaceae), including some Caribbean islands, northern Colombia and Venezuela, the same sectors of Ecuador and Peru previously mentioned, and in riverine environments linked to the sub-Andean Piedmont forests in northwestern Argentina but where the exsiccata might be of plants escaped from cultivation (O'Donell, 1959). In the east of the continent it occurs in the Caatingas and Misiones nuclei, and some odd appearances in the Amazon River valley area (around Santarem and Belém) have to be taken into account (Fig. 7B). This pattern is also followed in part by *Peltophorum dubium* (Spring.) Taub. (Leguminosae), which has been recorded for seasonal forests in Venezuela, but is more frequent in the east of the continent, namely in the caatingas, in mesophilous forests in Minas Gerais, São Paulo and Paraná, in the upper Uruguay River valley in Santa Catarina, and it has been frequently collected in eastern Paraguay. Once again this species is entirely absent from the chaco, only to reappear in Yungas-like areas close to Santa Cruz de la Sierra in Bolivia (Fig. 7C).

A similar situation, but in this case with the component elements segregated as varietal taxa, occurs in the caesalpinioid *Senna spectabilis* (DC.) Irwin & Barneby (Irwin & Barneby, 1982). The variety *spectabilis* extends from coastal Venezuela to Andean valleys in the Mérida area of the same country and the Magdalena and Cauca river valleys in Colombia, and then reappears in seasonal formations in Ecuador and further south in dry valleys in the Peruvian Andes (Fig. 7D). This variety is also a conspicuous member of the Yungas forests in Bolivia, and of the deciduous piedmont forests in southern Bolivia and northwestern Argentina where it is called "carnaval." As usual in this kind of distribution pattern this tree is entirely absent from the Chaco, only to reappear in eastern Paraguay. The other taxon, variety *excelsa* (Schrader) Irwin & Barneby, is virtually restricted to the caatinga in northeast Brazil, where it is called "canafistula."

The shrub to small tree *Solanum granulosoleprosum* Dunal (Solanaceae) shows a similar distribution (Fig. 8A). It has been collected in northern Colombia and Guyana, is absent from the Amazon but reappears in the caatingas of Bahia and Minas Gerais, and further south in the mesophilous forests of Rio de Janeiro, Paraná, and Santa Catarina, and also extends into adjoining Paraguay and northeastern Argentina, particularly in the Austro-Brazilian Transitional forest (Prado, 1991). As usual, it is absent from the Chaco but occurs in the eastern slopes of the Andes in northwestern Argentina and Bolivia.

## Restricted Arc Distributions

Some caatinga species have relatively widespread distributions but do not show the full sequence of links with other seasonal formations as do most of the cases considered above. Such species can be considered as having a restricted distribution, in which the third Piedmont nucleus is either lacking or very fragmentary. Several examples occur in the genus *Aspidosperma* (Apocynaceae). One such case is *A. pyrifolium* Mart. (Fig. 8B), which has been reported for Cerro León in Paraguay (Ramella & Spichiger, 1989). It is a characteristic species of the caatingas that spreads extensively into Minas Gerais, but then there is a disjunction with the populations on the river Paraguay. There is also a puzzling exsiccatum from Faro (Marcondes-Ferreira, 1988), in the Pará state,

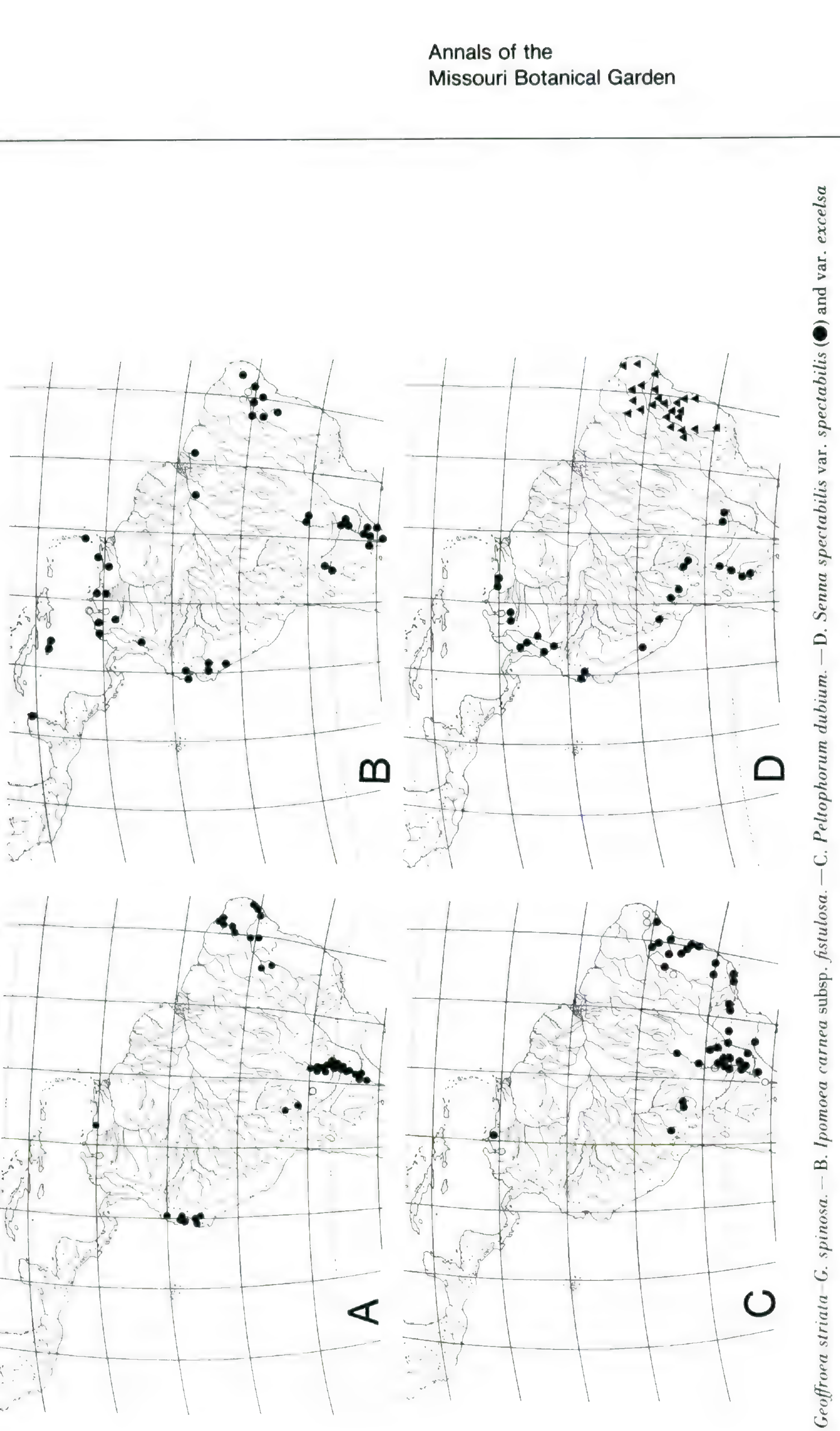


FIGURE 7.—A. *Geoffroea striata*–C. *Peltophorum dubium*.—D. *Senna spectabilis* var. *spectabilis* (●) and var. *excelsa* (▲).

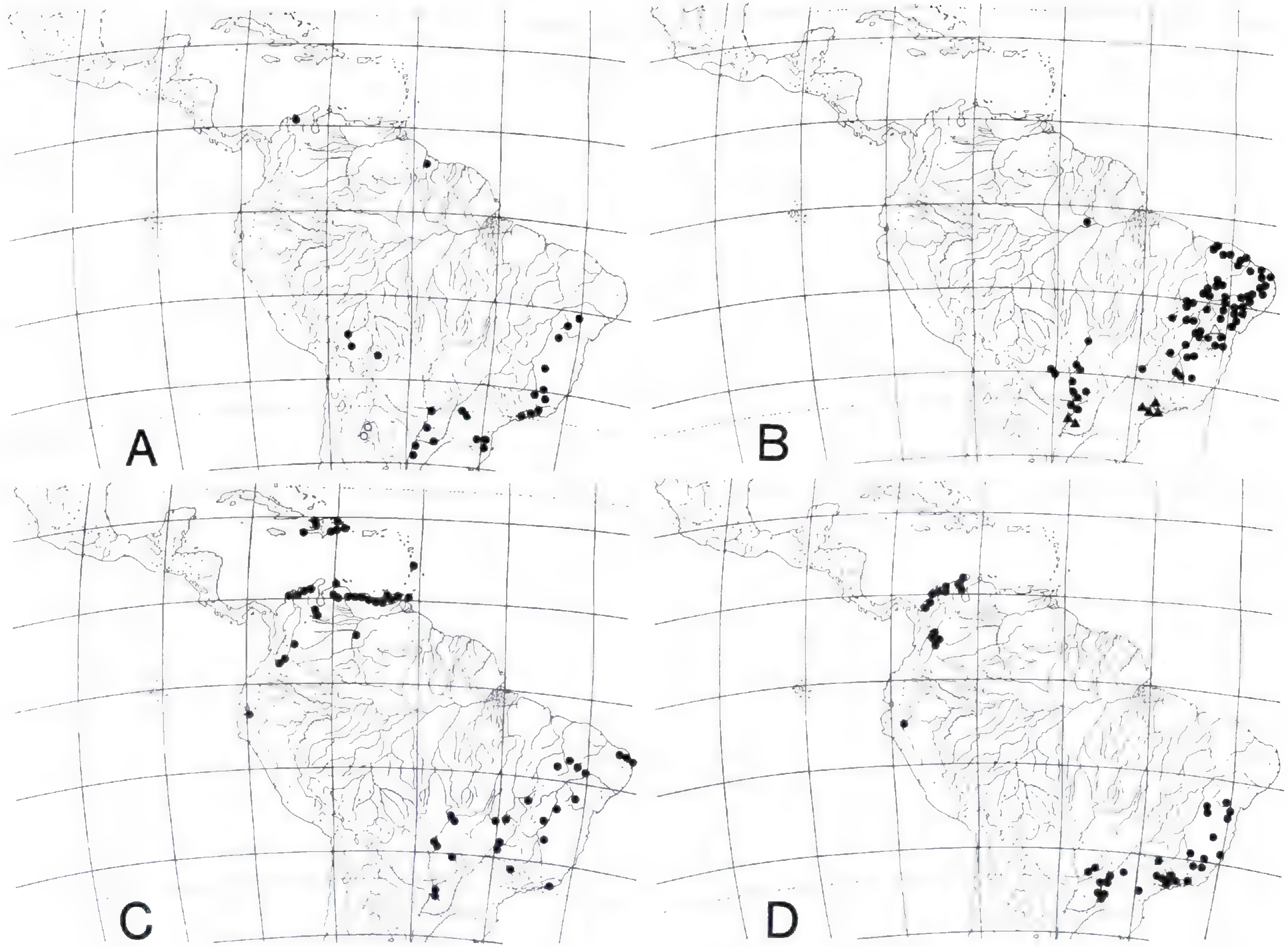


FIGURE 8[1].– A. *Solanum granuloso-leprosum*.—B. *Aspidosperma pyrifolium* (●), *A. riedelii* subsp. *riedelii* (▲) and subsp. *oliganthum* (△).—C. *Aspidosperma cuspa*.—D. *Aspidosperma polyneuron*.

a locality in a small sector of the Amazon valley where several other caatinga elements (Andrade-Lima, 1959) have also been collected (see further comments below). The tree *Aspidosperma riedelii* Müll. Arg., which has been treated by Marcondes-Ferreira (1988) as comprising two subspecies, subspecies *oliganthum* (Wood.) Marc.-Ferr., a Bahian endemic, and subspecies *riedelii* with two disjunct localities in the forests of São Paulo and in central Paraguay (Fig. 8B), shows a similar but more fragmented pattern. *Aspidosperma cuspa* (Kunth) Blake (Fig. 8C), which has been collected in the dry forests of Hispaniola and Martinique, is also a common tree in the dry Caribbean sectors of Colombia and Venezuela, countries in which it also extends to some dry, inter-Andean valleys. It reappears in southwestern Ecuador (Woodson, 1951), and at nearly the same latitude but on the opposite side of the continent in Rio Grande do Norte (northeast Brazil). A rather infrequent plant in the Caatingas nucleus, it is found scattered in the cerrado of central Brazil, and on rock outcroppings of the Cordillera de Altos in Paraguay (Marcondes-Ferreira, 1988). The taxonomically closely related *A. polyneuron* Müll. Arg. (Fig. 8D) parallels in part the distribution of *A. cuspa*, since it has been collected from the western half of the dry Caribbean sector and also in dry inter-Andean valleys in Colombia, but it has not been recorded so far from the eastern zone. No collections in Ecuador have been located, but it occurs in northern Peru in an area of similar vegetation to that of southwest Ecuador (Weberbauer, 1936; Harling, 1979). This species also occurs in the caatingas of Bahia (northeastern Brazil) and extends in a northeast-southwest arc through mesophilous forests in Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, and Paraná, to Paraguay and a very reduced area in north Misiones (Argentina).

The valuable timber tree *Balfourodendron riedelianum* (Engl.) Engl. (Rutaceae) occurs in the caatingas (Fig. 9A) and extends south to the planalto forests in Saõ Paulo and Paraná states, along the upper Uruguay River valley, and reaching eastern Paraguay and northeastern Argentina. Rather similar, two-nuclei distributions are found in the soft-wooded tree *Phytolacca dioica* L. (Phytolaccaceae), *Alseis floribunda* Schott (Rubiaceae), and *Astronium concinnum* Schott (Anacardiaceae) (Fig. 9B–D).

Another group of woody species is absent from the caatingas but occurs in the Misiones and commonly also in the Piedmont nuclei within the Pleistocenic Arc. These include two sapindaceous genera: the monotypic *Diatenopteryx*, with *D. sorbifolia* Radlk. (Fig. 10A), and the ditypic *Diplokeleba*, with one species, *D. floribunda* N.E. Brown, which is abundant on the Paraguay–Paraná system, while the other, *D. herzogii* Radlk., is known only from the type collection in Cabezas, Bolivia (Fig. 10B), most likely from the deciduous forests frequent in that area (Coro, 1956). A similar distribution is found in *Ziziphus oblongifolius* S. Moore (Rhamnaceae) (Fig. 10C), which is a frequent shrub in the north of the Paraguay–Paraná system (Prado et al., 1992), and cited by Herzog (1910) for Bolivia and Escalante (1946) for Orán in Salta (Argentina). Three species that are restricted to the Misiones nucleus are *Astronium balansae* Engler (Fig. 9D), *Ziziphus guaranitica* Malme (Fig. 10D), and *Maytenus ilicifolia* (Celastraceae) (Fig. 11A). Another taxon restricted to a single nucleus is the monotypic genus *Athyana* Radlk. (Sapindaceae), with *A. weinmannifolia* (Griseb.) Radlk., which is endemic to the piedmont forests of northwestern Argentina and southern Bolivia (Fig. 11A). The kind of distributions that is restricted to the second and third nuclei is also illustrated by the elegant rubiaceous tree *Calycophyllum multiflorum* Griseb., the dominant and characteristic species of the palo blanco forest in the piedmont of the sub-Andean chains (Fig. 11B), to which it gives its vernacular name, and which is also common in the River Paraguay area and in the Cerro León (Ramella & Spichiger, 1989). Some isolated populations of *C. multiflorum* have been occasionally found within the Chaco sens. str. (Castellanos, 1958; Morello, 1967; Morello & Adámoli, 1974).

Finally, ca. 180 woody species are endemic to the Caatinga province (Prado, 1991). Examples include *Ziziphus joazeiro* Mart. and *Z. cotinifolia* Reissek (Rhamnaceae) (Fig. 10C), *Fraunhoffera multiflora* Mart. (Celastraceae), the congenerics *Auxemma oncocalyx* (Allemão) Taub. and *A. glazioviana* Taub. (Boraginaceae), *Spondias tuberosa* Arruda (Anacardiaceae), *Cordia leucocephala* Moric. and *C. dardani* Taroda (Boraginaceae), and *Hymenaea eriogyne* Benth. (Figs. 11C, D, 12A, B).

### Taxa with More Complex Distributions

It is of considerable interest that a number of caatinga species show links with the Amazonian area. The outlying records for *Commiphora leptophloeos* and *Aspidosperma pyrifolium* noted above are two such cases. A congeneric example

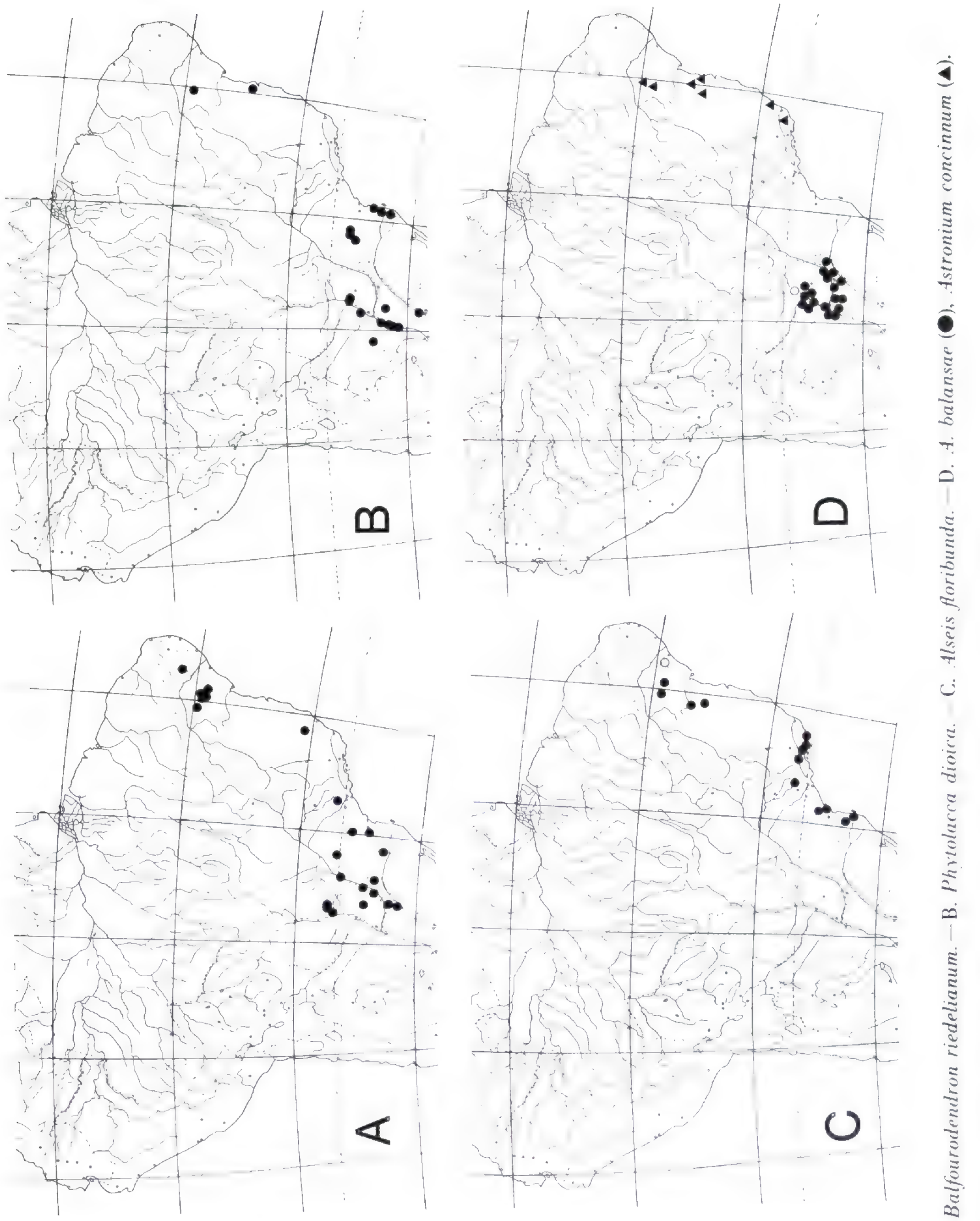


FIGURE 9.—A. *Balfourodendron riedelianum*.—B. *Phytolacca dioica*.—C. *Alseis floribunda*.—D. *A. balansae* (●), *Astronium concinnum* (▲).

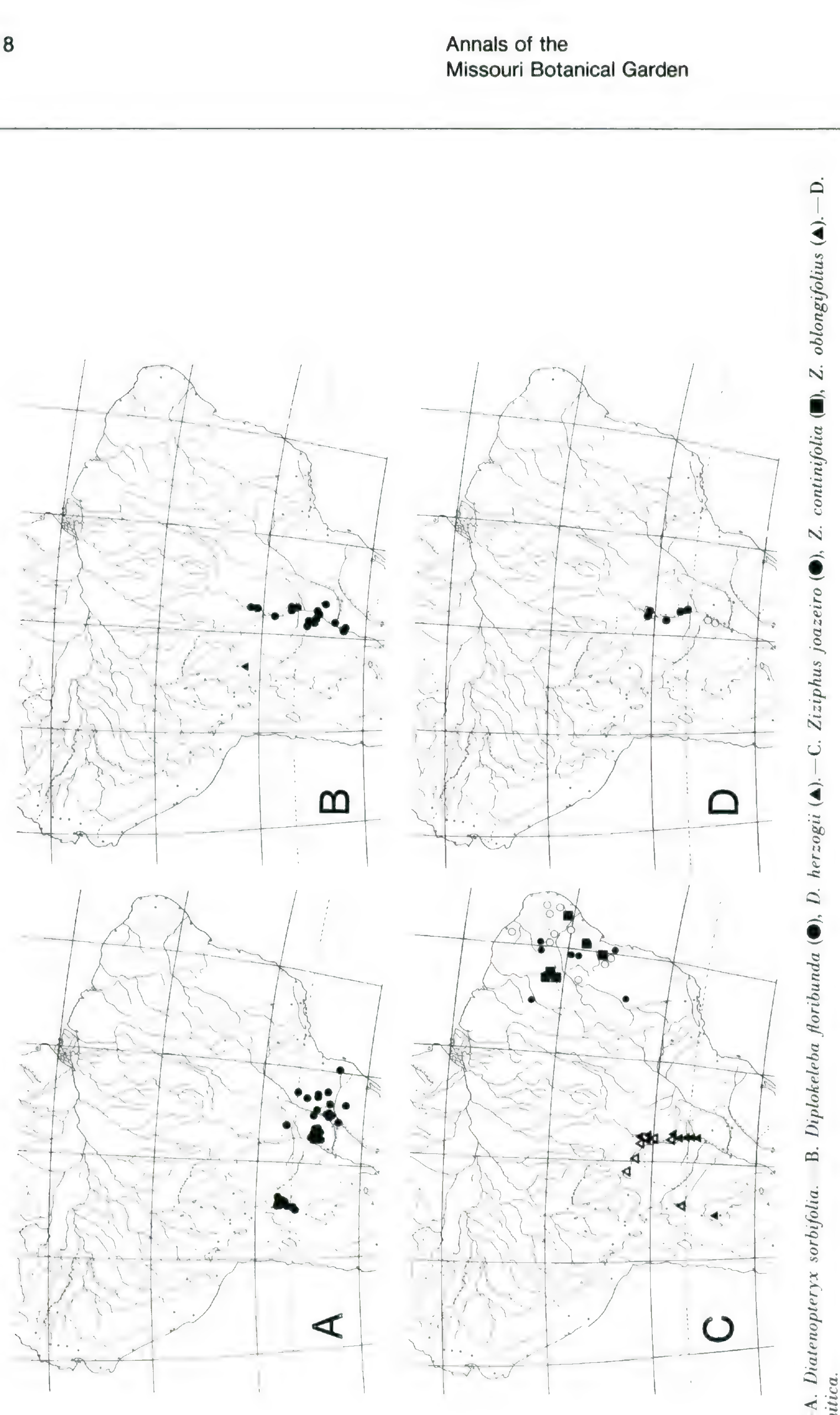


FIGURE 10[4].—A. *Diatenopteryx sorbifolia*. B. *Diplokeleba floribunda* (●), *D. herzogii* (▲).—C. *Ziziphus joazeiro* (●), *Z. continifolia* (■), *Z. oblongifolius* (▲).—D. *Ziziphus guaranitica*.

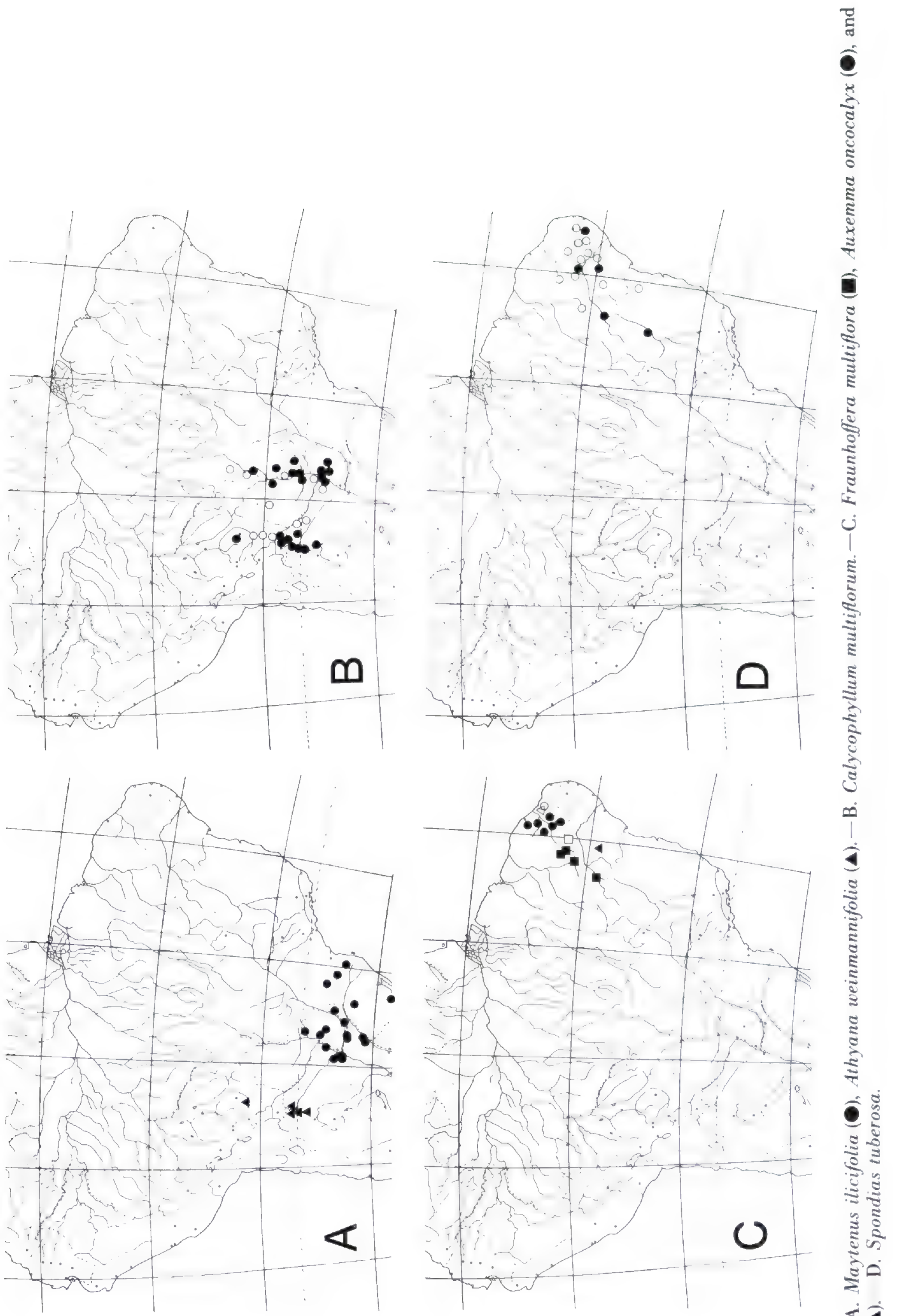


FIGURE 11[a].—A. *Maytenus ilicifolia* (●), *Athyana weinmannifolia* (▲).—B. *Calyophyllum multiflorum*.—C. *Fraunhoffera multiflora* (■), *Auxemma oncocalyx* (●), and *A. glazioviana* (▲).—D. *Spondias tuberosa*.

is *Aspidosperma discolor* A. DC., which occurs in Venezuelan Guayana and the Guianas, and which has been profusely collected in the lower and middle Amazon River valley and in Rondônia state, but it is also frequent in Bahian caatinga and in a central area of the cerrados (Fig. 12C). Another case is *Albizia polyantha* (A. Spreng.) Lewis (Leguminosae), which extends from the Guianas and Ilha de Maracá (Lewis & Owen, 1989), to the Amazon River valley and tributaries, and to the caatingas, the Paraguay–Paraná system and Cerro León (Fig. 12D). However, in a different category are species such as *Couepia uiti* (Mart. & Zucc.) Benth. (Chrysobalanaceae), which are essentially Amazonian elements, which extend via gallery forests into the cerrados and caatingas (Fig. 12B).

A number of species have more indistinct distribution patterns that include Amazonian localities. This sort of distribution is shown by a few caatinga species, although in each case they show fairly wide tolerance and also occur in more humid habitats. One such is *Coutarea hexandra* (Jacq.) K. Schum. (Rubiaceae), which also occurs along the Amazon River (Fig. 13A), and *Crateva tapia* L. (Capparaceae), which has been collected in the Amazon basin and also along the ephemeral watercourses in the caatingas (Fig. 13B). *Hymenaea courbaril* L. var. *courbaril* (Fig. 13C) and the outstanding caatinga tree *Tabebuia impetiginosa* (Mart. ex DC.) Standley (Fig. 13D) have similar distributions. Some such taxa are primarily restricted to seasonal habitats, such as *Myroxylon balsamum* (L.) Harms (Leguminosae) and *Poeppigia procera* C. Presl. (Leguminosae), although these species also appear in the Amazon (Fig. 14A, B), or as in the case of *Phyllostylon brasiliense* Capanema (Ulmaceae), in the Brazilian Atlantic rainforest (see distribution of the genus in Fig. 14C).

This distributional pattern is also followed (Fig. 14D) by another two-species complex: *Cordia alliodora* (Ruiz & Pav.) Oken–*C. trichotoma* (Vell.) Arráb. ex Steud. (Boraginaceae). Gibbs & Taroda (1983) studied this complex and concluded that both taxa should remain separate because of the different kinds of heterostylous conditions shown by plants of each species, together with differences in flower size, pollen grain size, and myrmecophily. However, these taxa have had a confusing history and have been treated as conspecific by some authors, while others have attempted to differentiate between them based on morphological characters such as leaf indumentum. This complex seems to show a high degree of ecological tolerance, with *C. alliodora* in particular showing fast-growing pioneer-type qualities, which may account for some aspects of its distribution. It extends from the semiarid Caribbean coast of Colombia and Venezuela, and the dry inter-Andean valleys of these countries, but also occurs in the more humid Orinoco River valley and even in the Amazon. From western coastal Ecuador and Peru, the distribution follows the more characteristic dry valley systems to reach the Yungas area in Bolivia. The specimens collected in northwestern Argentina in the sub-Andean Piedmont forests have been traditionally attributed to *C. trichotoma*, but from Gibbs & Taroda's (1983, fig. 1) point of view they must be regarded as *C. alliodora*, based both on morphology and geographical range. The specimens in the eastern half of the complex distribution are nearly all considered *C. trichotoma*, which thus extends from the caatingas, where this species can appear not only in the "sertão" but also in the wetter hills ("brejos"), to mesophilous forests on the Brazilian planalto (Minas Gerais, São Paulo, Paraná, and Santa Catarina), eastern Paraguay and northeastern Argentina.

Some species, such as *Platypodium elegans* Vogel (Leguminosae), that are more typical of the central Brazilian cerrado vegetation seem to partially shadow this distributional pattern (Fig. 15A). This species is a canopy tree in seasonal forest in Panama (Porter, 1973), and it is also present in Venezuela, but it then disappears in the whole of north and central South America to reappear in the caatingas, the cerrado in Goiás, Mato Grosso, Minas Gerais, and São Paulo, and further extends into eastern Paraguay and eastern Bolivia. Likewise, the anacardiaceous tree *Astronium fraxinifolium* Schott (Fig. 15B) is found in northern Colombia and Venezuela, and although it is absent from the caatingas sens. str., it has been recorded in semideciduous communities on higher ground within the general caatinga area. In central Brazil, it has been considered one of the indicator species of mesotrophic cerradão by Ratter et al. (1977), and it also extends to eastern Paraguay and central Bolivia. There is a surprising collection of this species in the Cañadón Platanillos, in central Paraguayan chaco, which must undoubtedly be linked to one of the watercourses that cross this region in a general west-east direction.

Finally, it should be emphasized that the distributions of the only three woody species (*Parkinsonia aculeata* L., *Sideroxylon obtusifolium* (Roem. & Schult.) Pennington, and *Ximenia americana* L.) that are common to the chaco and caatingas are meaningless in this context, since all three species have widespread distributions and

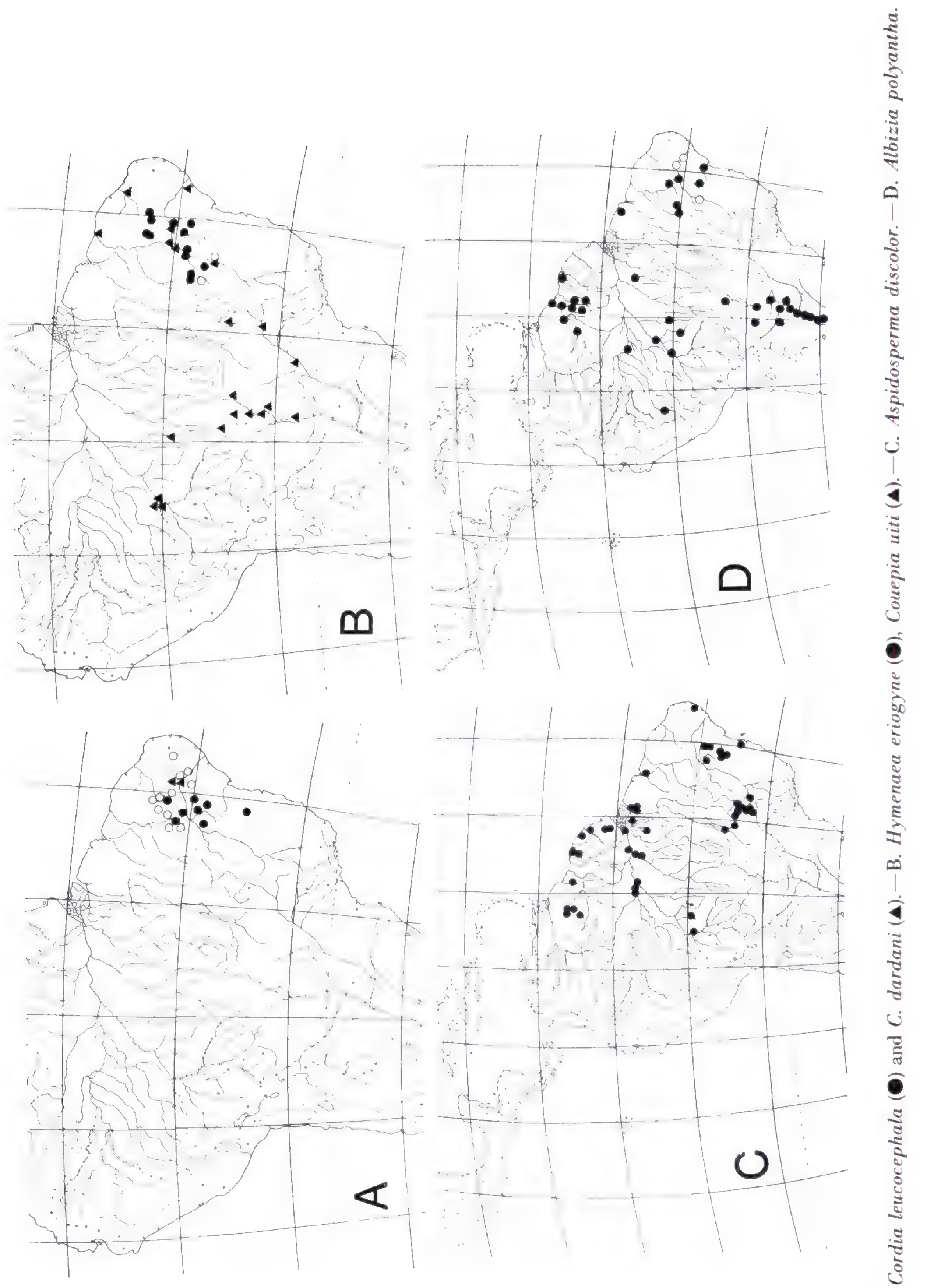


FIGURE 12[4].—A. *Cordia leucocephala* (●) and *C. dardani* (▲).—B. *Hymenaea eriogyne* (●), *Couepia uiti* (▲).—C. *Aspidosperma discolor.*—D. *Albizia polyantha.*

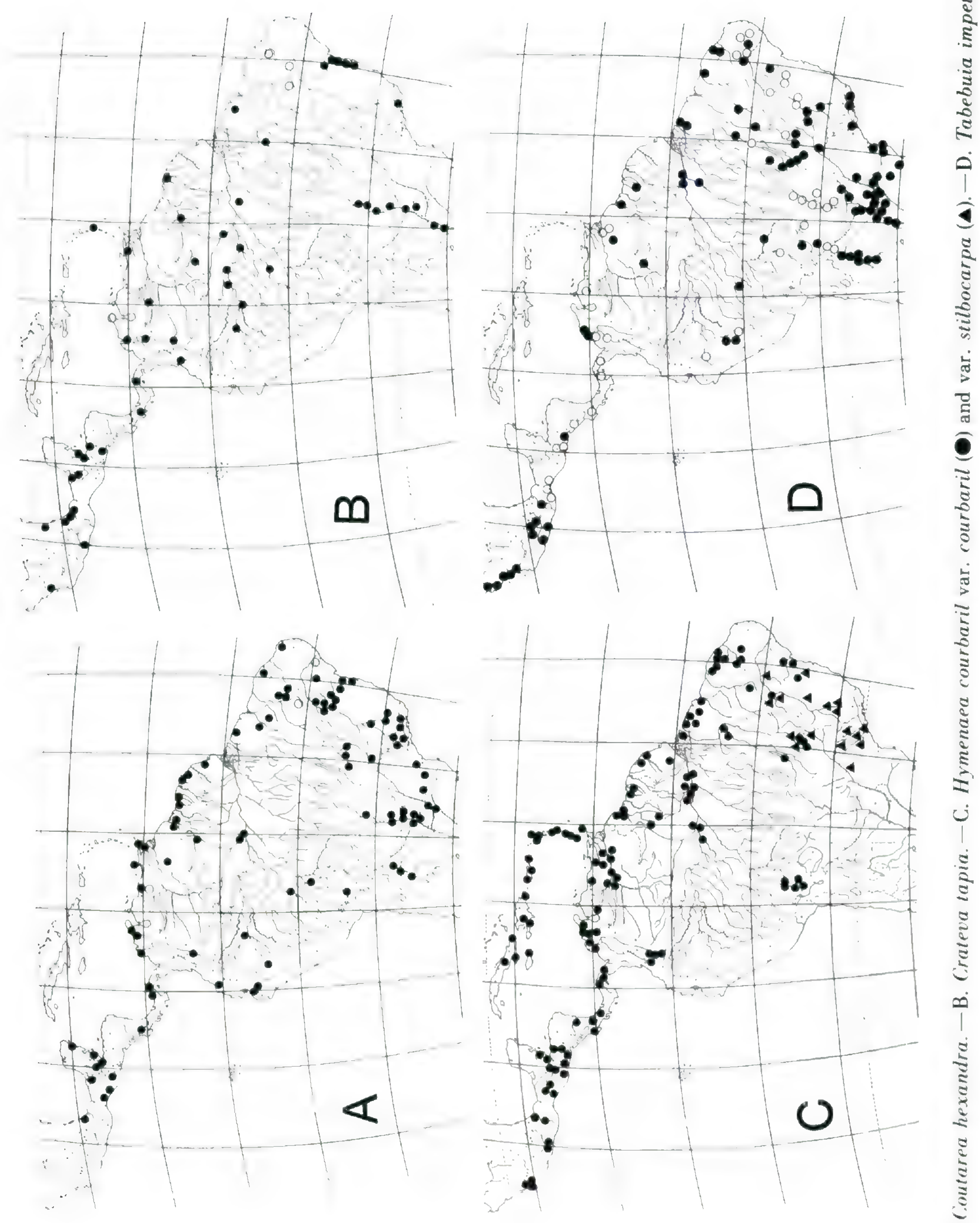


FIGURE 13.—A. *Coutarea hexandra*.—B. *Crateva tapia*.—C. *Hymenaea courbaril* var. *courbaril* (●) and var. *stilbocarpa* (▲).—D. *Tabebuia impetiginosa*.

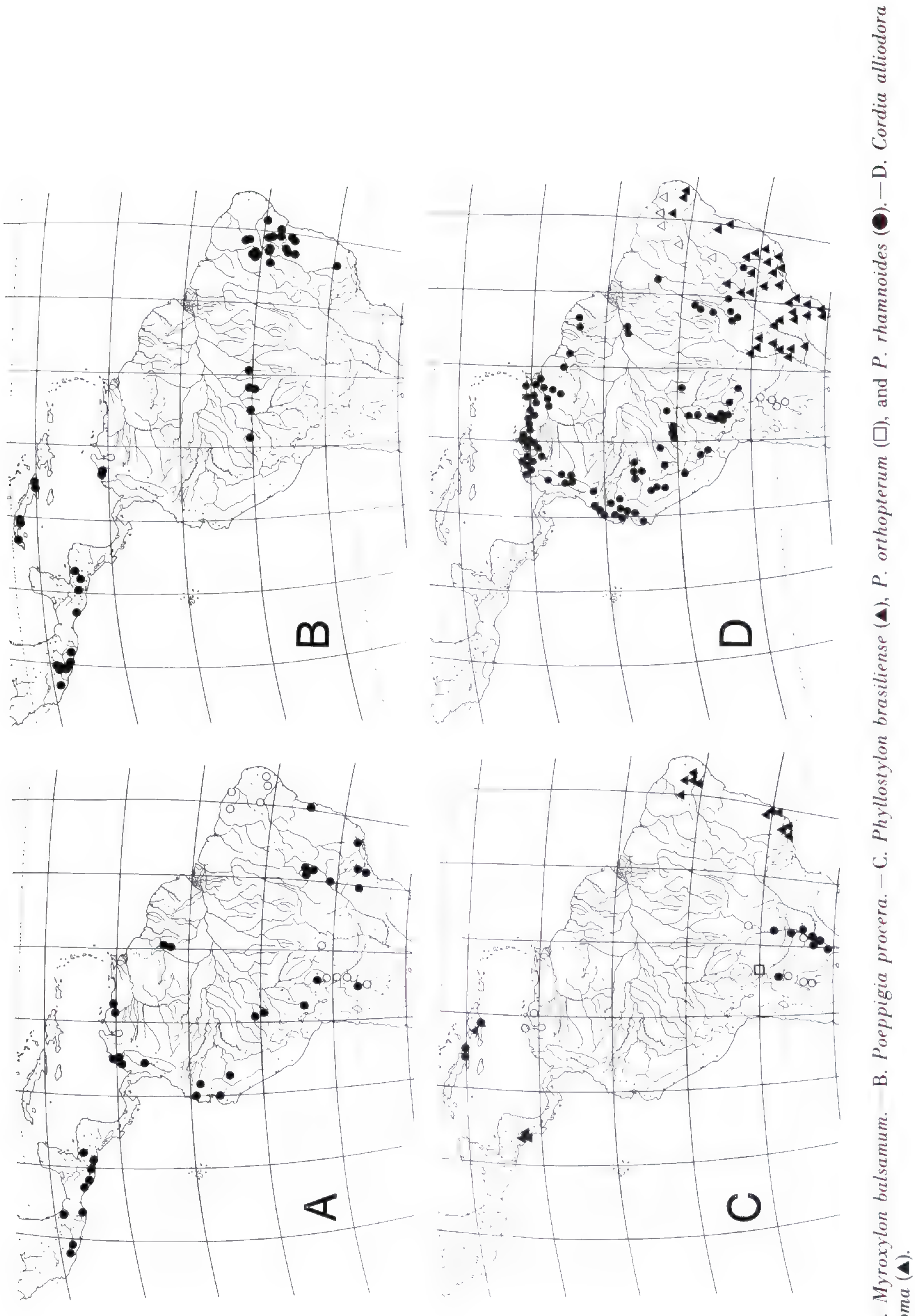


FIGURE 14[4].—A. *Myroxylon balsamum*. — B. *Poeppigia procera*. — C. *Phyllostylon brasiliense* (▲), *P. orthopterum* (□), and *P. rhamnoides* (●).—D. *Cordia alliodora* (●) and *C. trichotoma* (▲).

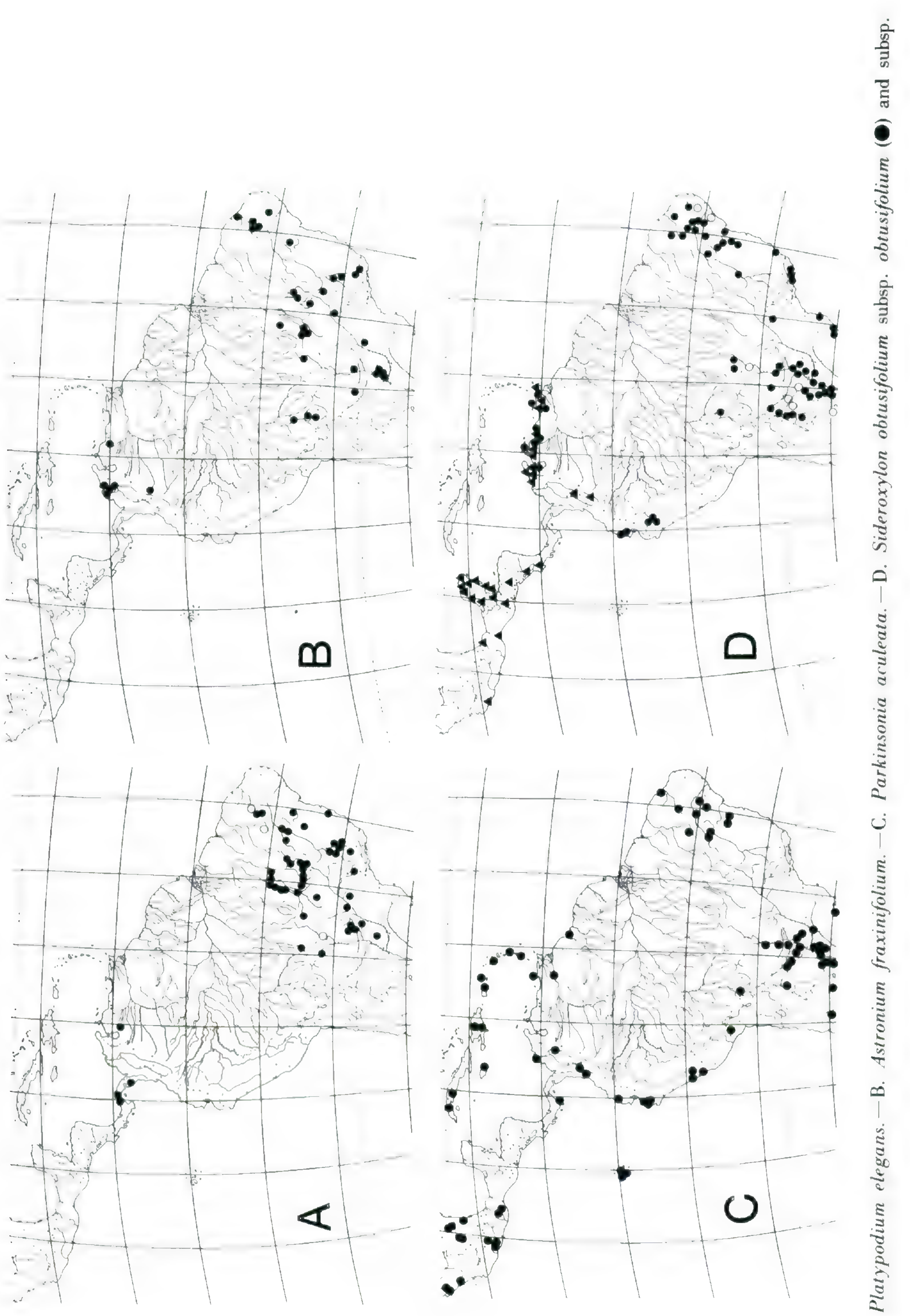


FIGURE 15[4].—A. *Platypodium elegans.*—B. *Astronium fraxinifolium.*—C. *Parkinsonia aculeata.*—D. *Sideroxylon obtusifolium* subsp. *obtusifolium* (●) and subsp. *buxifolium* (▲).

occur in diverse vegetation types. *Parkinsonia aculeata* (Leguminosae) is a very widespread ruderal plant whose ecological amplitude includes the Pacific coastal desert of Peru and the arid Monte province of Argentina (Fig. 15C). *Sideroxylon obtusifolium* (Sapotaceae) shows some fidelity to the seasonal formations, but together with the other two species it also occurs in temperate areas of South America (Fig. 15D). These species are also exceptional in that in addition to the chaco, they spread into areas such as Monte, or even Patagonia in the case of *Ximenia americana* (Olacaceae) (see map in Sleumer, 1984).

## Conclusions

The 80 or so taxa mapped in this analysis are all woody components of a series of dry seasonal woodland formations that occur in South America. This is a vegetation that seems to be mainly restricted to relatively mineral-rich soils. The present-day distributions of these species are considered to comprise fragmentary remnants of the once extensive forests that probably characterized the dry climatic maxima of the Pleistocene, and which are likely at that time to have extended into the Amazonian region, and also to have percolated into the Andean region, perhaps via the "Marañon gap," and established further links with the Caribbean–Guajira province, through northwestern Peru and eastern Ecuador.

The extant fragments of this seasonal woodland vegetation have their main nuclei in the Caatingas, Misiones, and Piedmont areas. Effectively, the woody and succulent flora of the caatingas comprises ca. 437 species, of which 228 species are certainly nonendemics (Prado, 1991). Of these, some 62 species (27%) show floristic affinities to the Pleistocenic Arc type distribution, whilst no other coherent distribution patterns were evident for the remaining nonendemic species. Equally notable, some 51 species (19.4%) of the ca. 263 woody and succulent species found in the piedmont forests of northwestern Argentina and southern Bolivia are also found in the caatingas, while a further 42 (16%) piedmont species show links with the Misiones nucleus and calcareous woodlands peripheral to the Brazilian cerrados (Prado, 1991).

Characteristically, these species distributions present a lacuna in the area of the chaco, and only sparse representation in the cerrado, with most seemingly cerrado representatives of this group actually restricted to calcareous outcrops. Indeed, the essentially distinct nature of typical Brazilian cerrado vegetation from other seasonal, semideciduous woodlands is striking, in sharp contrast to the clear floristic links between such seasonal woodland and the rather distinctive vegetation of the calcareous islands within the cerrado general area, as first emphasized by Ratter et al. (1978).

The caatinga-type seasonal woodlands also show intriguing links with some areas in the Amazonian, as well as the Caribbean and Venezuelan–Central American, regions, and with some species having isolated populations surviving in dry valleys of the east slopes of the Andes. It is unfortunate that, probably because of their occurrence on agriculturally desirable, good-quality soils, these seasonal forests in South America have suffered considerable devastation in the past, and continue to bear the brunt of agricultural expansion in the region. This applies particularly in the case of the piedmont woodlands of northwestern Argentina, and to the isolated areas of "mata calcárea" on base-rich outcrops scattered within the Brazilian cerrado area. A coherent conservation policy for selected areas of these seasonal forests areas is urgently needed.

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# DIVERSITY PATTERNS AND BIOMASS OF EPIPHYTIC BRYOPHYTES AND LICHENS ALONG AN ALTITUDINAL GRADIENT IN THE NORTHERN ANDES[1]

*Jan H. D. Wolf*[2]

## Abstract

The difficult accessibility of the canopy of tropical rainforests is probably one of the main reasons why information about the nonvascular tree crown flora is scarce. In this paper full attention is paid to the epiphytic bryophytes and lichens of 59 bark type selected canopy trees, divided over 15 sites along an altitudinal transect ranging from 1,000 to 4,130 m in the Central Cordillera, Colombia. Species-area curves indicated that sampling at each investigated site (altitude) was adequate within the restrictions imposed by the sampling method. Ordination analysis revealed that altitude as a complex ecological factor explained most of the variation in the data. Alpha and beta diversity patterns along the gradient were different for mosses, liverworts, and macrolichens. As to liverworts, species richness reached its peak of approximately 100 taxa per altitude at a mid-altitudinal range from 2,550 m to 3,190 m. The distribution of individual taxa showed that the belt of greatest liverwort richness coincides with a contact transition zone. Several hypotheses (mass effect, ecological equivalency, and species overlap) predict highest species diversity at such a transition zone. All are based on the assumption that community composition results from between community interactions rather than from within community (niche) relationships. The validity of this presumption is further indicated by the low number of liverwort taxa (20.5%) exclusive to the belt of greatest richness, assuming that habitats are saturated. Species turnover appears greater for bryophytes on this tropical mountain than on temperate mountains in North America. The general increase in biomass of nonvascular canopy subsamples with altitude coincides with a rise in humidity.

The study of species diversity (species richness) is a central theme in both theoretical and applied ecology. Following Whittaker (1977), point diversity is defined as the species richness of a single subsample taken on a host tree and alpha diversity as the number of species of all the subsamples taken at four host trees per altitude. Beta diversity may be defined as the extent of species replacement along an environment gradient (MacArthur, 1965; Whittaker, 1960, 1972, 1977).

Origin and maintenance of local diversity may be explained in two ways: as a result from (1) processes (niche relations among species) within the community (MacArthur, 1965; Whittaker, 1977; Connell, 1978; Huston, 1979), or from (2), at least in part, propagule influxes from neighboring sites (Shmida & Wilson, 1985). Slack (1977) and Watson (1980) suggested that in bryophyte communities species diversity results more from successful colonization and establishment than from competition-related interactions.

It is generally accepted that tropical regions are richer in species than temperate areas (e.g., Pianka, 1966), but documentation of diversity patterns within the tropics is still rare (Gentry, 1982), in particular for nonvascular plants (Maury-Lechon et al., 1984). Species richness studies of various organisms along altitudinal gradients in the tropics have demonstrated three major patterns: (1) A decrease of species richness with altitude for woody

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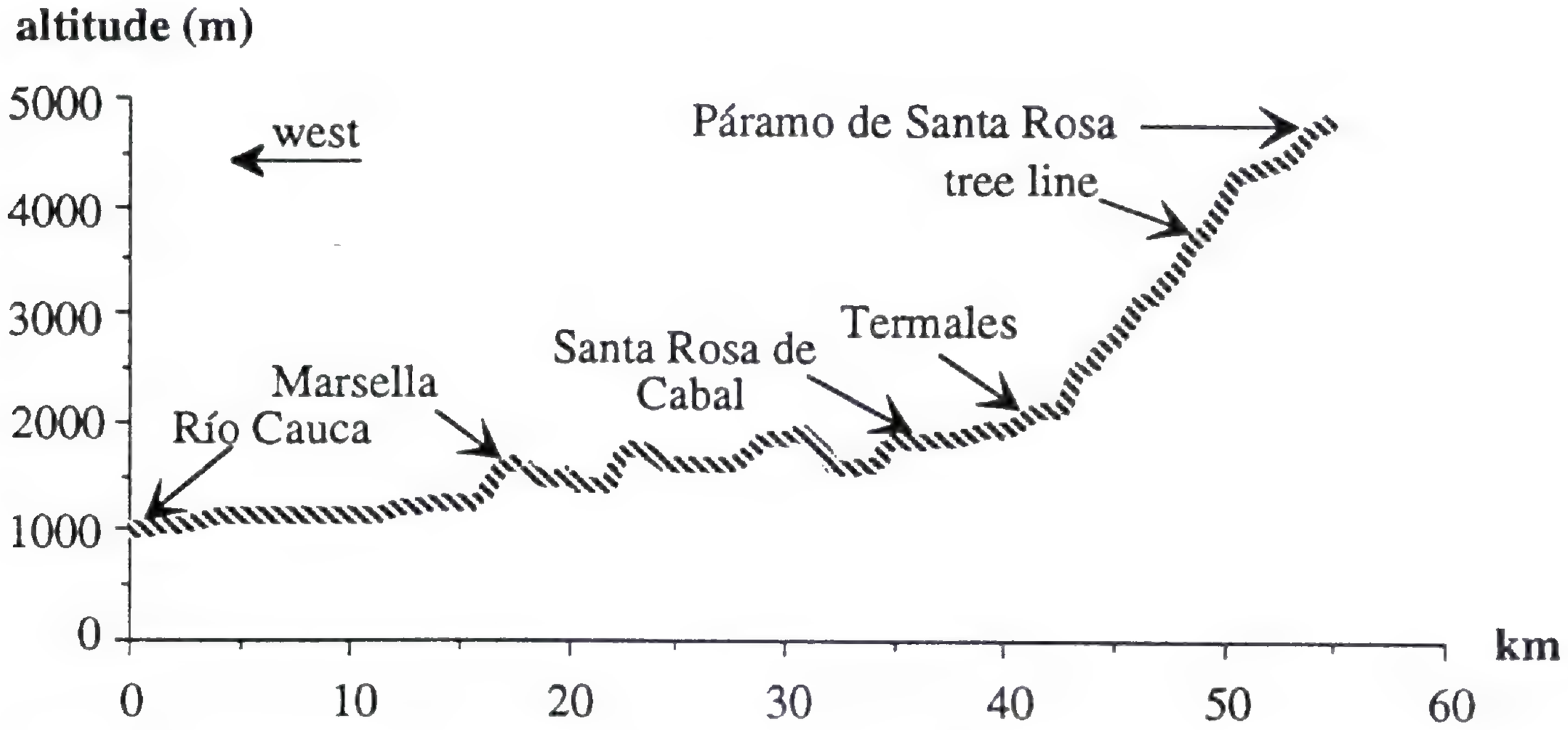



FIGURE 1. Longitudinal section of the west slope of the TPN-transect; redrawn from Thouret (1983).

phanerogams (Gentry, 1988), herpetofauna of leaf litter (Scott, 1976; Fauth et al., 1989), and anuran amphibians (Duellman, 1988). (2) A maximum of species richness at higher altitudes for mosses (Gradstein & Frahm, 1987; Frahm, 1987a), liverworts (Gradstein & Weber, 1982), bryophytes (Gradstein et al., 1989), and lichens (Sipman, 1989). The latter two studies were conducted along the transect treated in this study and included both terrestrial and epiphytic (mainly tree base) sampling. (3) A maximum of species richness at intermediate altitudes for birds (Terborgh, 1977), insects (Janzen, 1973), vascular epiphytes (Sugden & Robins, 1979, and assumed by Gentry & Dodson, 1987), bryophytes (Enroth, 1990), and liverworts (Wolf, 1989). Gradstein & Pócs (1989) also documented higher bryophyte (excluding epiphylls) species numbers at intermediate (1,500–2,600 m) altitudes in the Sierra Nevada de Santa Marta. Highest cover values of both terrestrial and epiphytic (1–3 m) bryophytes were found at Santa Marta at altitudes over 2,600 m (van Reenen & Gradstein, 1983). The increase of nonvascular epiphytes with altitude is a common feature of tropical mountain areas worldwide (Grubb, 1977; Grubb et al., 1963; Pócs, 1980; Frahm, 1987b), and it has been suggested that it is paralleled with an increase in species richness (Richards, 1984, 1988).

Beta diversity, which focuses on the qualitative differences between habitats, has received much less attention than alpha diversity. As far as I know, only two studies on beta diversity of cryptograms along an altitudinal gradient are available, both concerning bryophytes in temperate North America (Slack, 1977; Lee & La Roi, 1979). Other studies (Robinson et al., 1989; Oksanen, 1983) addressed the difference in response of bryophytes and lichens along other than altitudinal gradients.

The aim of this paper is the recording and assessment of species richness, distribution, and biomass of epiphytic bryophytes and lichens along an altitudinal transect in the northern Andes. The possible role of interactions between sites within the altitudinal macro-gradient on epiphytic species richness will be examined. For the first time in tropical mountains full attention was paid to the flora of the forest canopy.

## Study Area

The study was carried out along an altitudinal transect (1,000–4,130 m) on the western slope of the Colombian Central Cordillera (ca. 4°50′N, 75°30′W) in the watershed of the Río Otún. This transect is known from previous ecological studies as the "Transecto Parque Los Nevados" (van der Hammen et al., 1983, 1989; Veneklaas, 1990; Vis, 1989). Data on the bryophyte and lichen flora of the study area are provided by van Reenen (1983), Gradstein et al. (1989), and Sipman (1989).

The mountain slope is not steep from the Río Cauca valley floor at 1,000 m up to Termales at ca. 2,000 m altitude (Fig. 1). Above, there is a sudden increase in slope. The upper tree line is found at 3,700 m, but locally at higher elevations a dwarf forest (6–8 m) dominated by *Polylepis sericea* Wedd. and *Diplostephium violaceum* Cuatrec. may be present.

The watershed exhibits a bimodal yearly distribution of rainfall, coinciding with the passing of

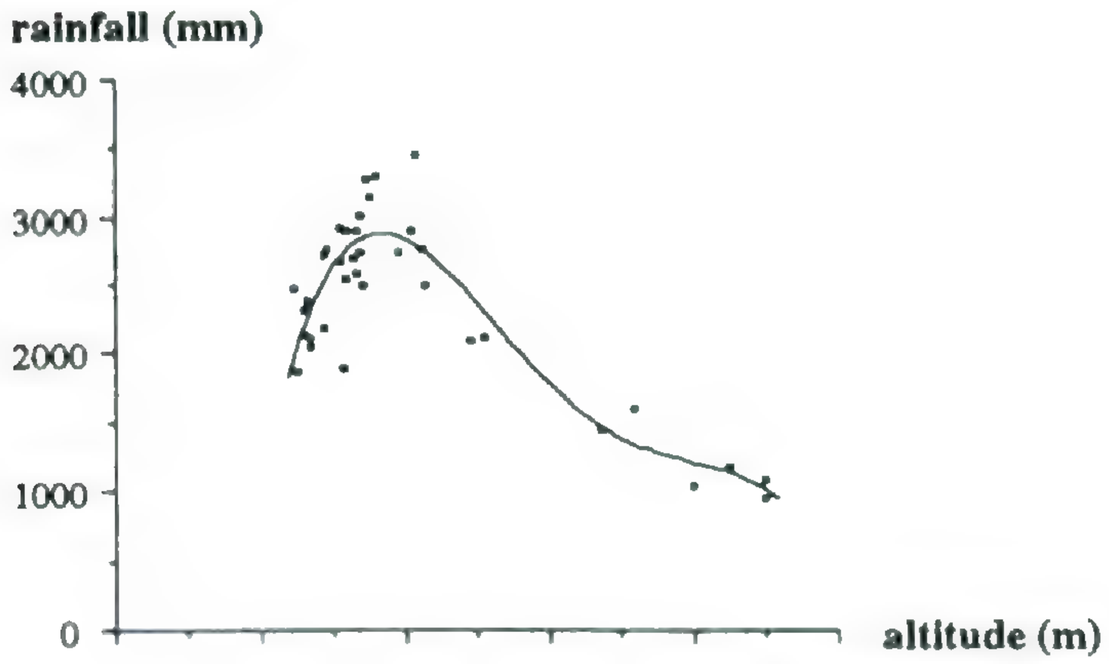



FIGURE 2. Annual rainfall distribution per altitude, after van de Weert et al. (1986).

the Intertropical Convergence Zone (Pérez, 1983). Rainfall data for a period of over 20 years from nearby meteorological stations, Matecaña Airport (1,342 m) and El Cedral (2,120 m), show that local rainfall exceeds 100 mm/month, even during the "dry" season (van der Weert et al., 1986).

Differences in precipitation and air humidity data from meteorological stations in the area seem to be largely correlated with differences in altitude. Based on climatic data from more than 40 stations at altitudes of 1,020–4,500 m, van de Weert et al. (1986) found a linear decrease of mean daily temperature in the watershed with altitude (0.63°C/100 m) and an annual precipitation maximum at around 2,000 m (Fig. 2).

## METHODS

Fieldwork was carried out from August 1985 to December 1986 and during the second half of 1988.

Diurnal variation of temperature and relative humidity at different altitudes (1,725 m, 2,150 m, 2,460 m, 2,970 m, 3,370 m, and 3,670 m) was recorded by Lambrecht thermohygrographs hung in white-painted, wooden, collapsible housing that was open at the bottom and had slots at the sides, allowing good aeration but avoiding sunlight at the measuring equipment. The housing was placed outside the forest at 2 m above ground level. At 3,370 m, where a clearing was not available, the thermohygrograph was placed about 1 m above the tree canopy hanging from an upright pole tied in the tree crown. As hair extension in the hygrograph is maximal at 95% relative humidity, humidity values higher than 95% could not be recorded.

Even though time of registration was limited to 2–3 weeks per site, the small seasonal variations in temperature and relative humidity (van der Weert et al., 1986) permitted a good impression of diurnal patterns.

Hemispherical photographs (167°) were taken with a superwide angle lens mounted on the front of the 24-mm lens of a standard 35-mm camera, to determine light conditions within the forest. Two perpendicular levels attached to the camera body permitted precise vertical canopy photographs. Diffuse site factors (Anderson, 1964), which provide a reasonably accurate estimate of the mean percentage of diffuse light passing through the canopy, were determined from the photographs using the method described by Anderson (1964). The amount of direct sunlight at the sites was not estimated, since data on the variation in periods of sunshine along the transect were not available.

### SAMPLING

At altitudinal intervals of ca. 200 m four trees were selected for investigation. Selected trees had to be (1) full-grown with their crowns reaching the average tree crown level (canopy); (2) of a common species in the forest; and (3) without a scaling, very hard, very smooth, or very coarse bark (at 4,130 m an exception was made for dominant *Polylepis* trees, which have a flaky bark). Additionally, they were not to be located near the edge of the forest, near a stream, on very steep terrain, on a ridge or in a gulley, or next to a previously sampled tree. Taxonomical affinity of host trees was not considered. Host-preference of epiphytes is often regarded of minor importance in wet montane tropical forests (e.g., Richards, 1984; Smith, 1982).

An effort was made to locate forests where disturbance was minimal. At 1,000 m it was not possible to find forests not disturbed by humans, but also at higher altitudes (e.g., at 2,130 and 2,460 m) much forest seemed disturbed, as evidenced by fast-growing "weedy" tree species like *Brunellia occidentalis* Cuatrec., *Solanum inopinum* Ewan, and by treeferns (Cyatheaceae). Since in these higher forests disturbance by humans was not apparent, these trees appear to form a natural element of the forest, perhaps due to the frequent occurrence of landslides (pers. obs.).

Epiphytic, excluding epiphyllous, vegetation was sampled on 59 trees (only three trees at 1,000 m). On each tree ca. 10 subsamples were taken at habitats such as tree base, trunk, inner crown, middle crown, and the outer branches, wherever a clear change in structure or in species quality of the epiphytic vegetation occurred along the vertical within-tree gradient. Subsamples taken on branchlets in the outer tree crown covered a smaller

area than on tree bases; subsample area varied from a few to over 20 $dm^2$. Branches were sampled above and aside only, epiphytes growing in the rain shadow underneath were excluded. Prior to removal from the bark of each subsample as a whole, information was gathered about the location, plot size, and percent cover of the dominant species relative to the area of the upper half-cylinder of the branch segment. The epiphyte communities are described in detail in Wolf (1993a, b).

A first impression of the species composition of 596 subsamples taken was obtained in the field laboratory in order not to miss tiny bryophyte species that are easily overlooked when dry. Subsequently, organic debris was separated and all subsamples were oven-dried at 70°C, weighed (excluding phanerogams), and sent to the laboratory in the Netherlands, where they were reexamined for hitherto not-found species and to check the field identifications. Biomass in this study is defined as the (dry) weight of living plants, excluding accumulated suspended organic soil. Parts of plants were assumed to be living whenever they were recognizable as plant structures and included brownish bryophyte bases of tall turf-forming species.

Some 1,600 botanical collections were deposited in the Herbarium of the Instituto de Ciencias Naturales (COL), Bogotá, with duplicates in the Herbarium of the University of Utrecht (U). Some duplicates were sent to specialists for identification.

Each tree was climbed using slightly modified rope climbing techniques, as described by Perry (1978a) and ter Steege & Cornelissen (1988). With a hunting bow, an arrow with a nylon line attached was shot through the tree crown and the tree was climbed with jumars along a mountaineering rope.

## SPECIES IDENTIFICATION

Species identification is problematical for groups of organisms that have not been adequately treated systematically. For the lichens this concerns in particular the genera *Sticta*, *Lobaria*, *Leptogium*, and *Usnea* and for bryophytes some members of the Lejeuneaceae (subfamily Lejeuneoideae), Plagiochilaceae, and Bryaceae. Some unidentified species were given provisional names (e.g., *Lejeunea* sp. *A*. *Lejeunea* sp. *B*) and included as such in the analysis; others could not be recognized as individual species and were grouped in higher taxonomic ranks (e.g., *Sticta* spp.; Lejeuneaceae). Furthermore, species were grouped when they could only be differentiated from their close allies in a fertile state, like most sterile crustose lichens, but also some bryophytes, e.g., *Omphalanthus filiformis* (Sw.) Nees and *O. platycoleus* Herz (Gradstein et al., 1981). Finally, two pleurocarpous moss species, *Ctenidium malacodes* Mitt. and *Mittenothamnium reptans* (Hedw.) Card, and all species of the crustose lichen family Graphidaceae were lumped, because they could only be separated after detailed microscopic investigation and were regularly found to grow intermixed.

The resulting amount of species-grouping into higher taxonomic ranks may be roughly estimated from the variety within each rank. Thus, for example, the 65 taxa of Lejeuneaceae used in the analysis are believed to represent ca. 70% of total Lejeuneaceae species present.

Nomenclature follows recent checklists of liverworts (Gradstein & Hekking, 1979), mosses (Churchill, 1989), and lichens (Sipman, 1989) or the latest taxonomic works, when available.

## DATA COMPUTATION

To make a meaningful evaluation of alpha and/or beta species diversity patterns, two requirements should be met:

(1) Adequate sampling. Minimum area (cumulative species vs. number of subsamples) curves were constructed (Fig. 3) and the rapid leveling of the curves shows that the minimum area of epiphytic bryophytes and lichens is small, agreeing with Gradstein et al. (1990), who found that sampling of epiphytic bryophytes in mixed tropical lowland forest of French Guiana yielded only few (1–3) additional species per tree when more than five trees were sampled.

(2) Establishment that the gradient under investigation, i.e., altitude, is indeed the major environmental factor determining species distribution. For that purpose, ordination analysis, using presence/absence data of species, was carried out using Detrended Correspondence Analysis, DECORANA (Hill, 1979; Hill & Gauch, 1980). A graphic representation of the first two axes is shown in Figure 4. The first axis of ordination of the sites shows a relatively high eigenvalue (0.652), suggesting the presence of a clear species gradient indicating the site variation. The second axis has a much lower eigenvalue (0.259), thus most variation can be explained by the gradient corresponding with the first axis. Eigenvalues of the third and fourth axes are 0.163 and 0.107, respectively.

Since the Spearman's rank coefficient for correlation calculated between the ordination rankings of the sites along the first axis of ordination and altitude was highly significant ($R = 0.993$; $P <$

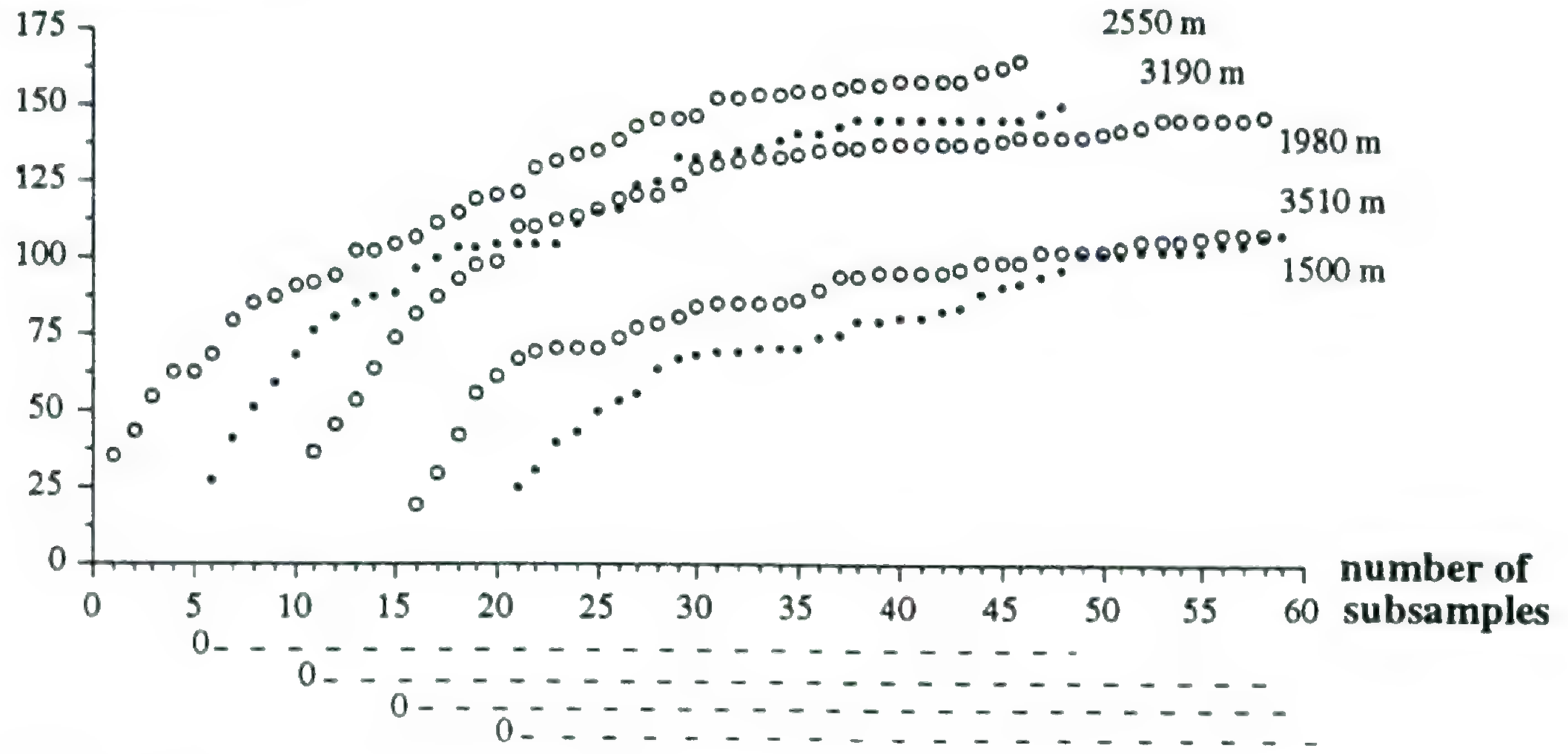



FIGURE 3. Cumulative species vs. number of subsamples (in random order) curves. The subsamples were taken on four trees per altitude.

0.001), it can be concluded that the variation in altitude explains most of the variation in the data. Therefore, it is felt permissible to consider species distribution to be continuous between highest and lowest altitudes where species were found. For further calculations this assumption was made, following Wilson & Shmida (1984).

Ordinations, using DECORANA, were performed for all data again, but also for macrolichens, bryophytes, mosses, and liverworts separately. The sites at 1,000 m and at 4,130 m were excluded, the lower site being much influenced by humans and the higher site, an outlier on the second axis in the first ordination (Fig. 4), not being part of the montane hillside forest. Crustose lichens were not considered because of the presence of many sterile unidentifiable species.

For unidimensional gradients the position of the sites on the first axis, as generated by DECORANA, has been shown to be a reliable estimate of beta diversity (Økland, 1986). Beta diversity was furthermore quantified using Sørensen's Coefficient of Community (1948) and a measure proposed by Wilson & Shmida (1984), which combines features of measures proposed by Cody (1975) and Whittaker (1960):

Sørenson (1948)

$$\text{C. C. Sørenson} = 2s/(a + b)$$

Wilson & Shmida (1984)

$$\text{"beta turnover"} = [g(H) + l(H)]/2\alpha;$$

where s = number of species found at both sites, a = number of species at site A, b = number of species at site B, g(H) and l(H) are number of species gained or lost respectively over the gradient, and $\alpha$ = average site richness.

Wilson & Shmida (1984) recommended the use of their index when sample (site) data can be arranged along a single overriding gradient, as in our case.

Previous studies on beta diversity of bryophytes have used the number of half changes in community composition along an elevational gradient (coenocline in the terminology of Whittaker), following Whittaker (1960). For reasons of compatibility the same method was used. Coefficients of Community, CC (Sørensen, 1948), were calculated for sites at different intervals along the coenocline.

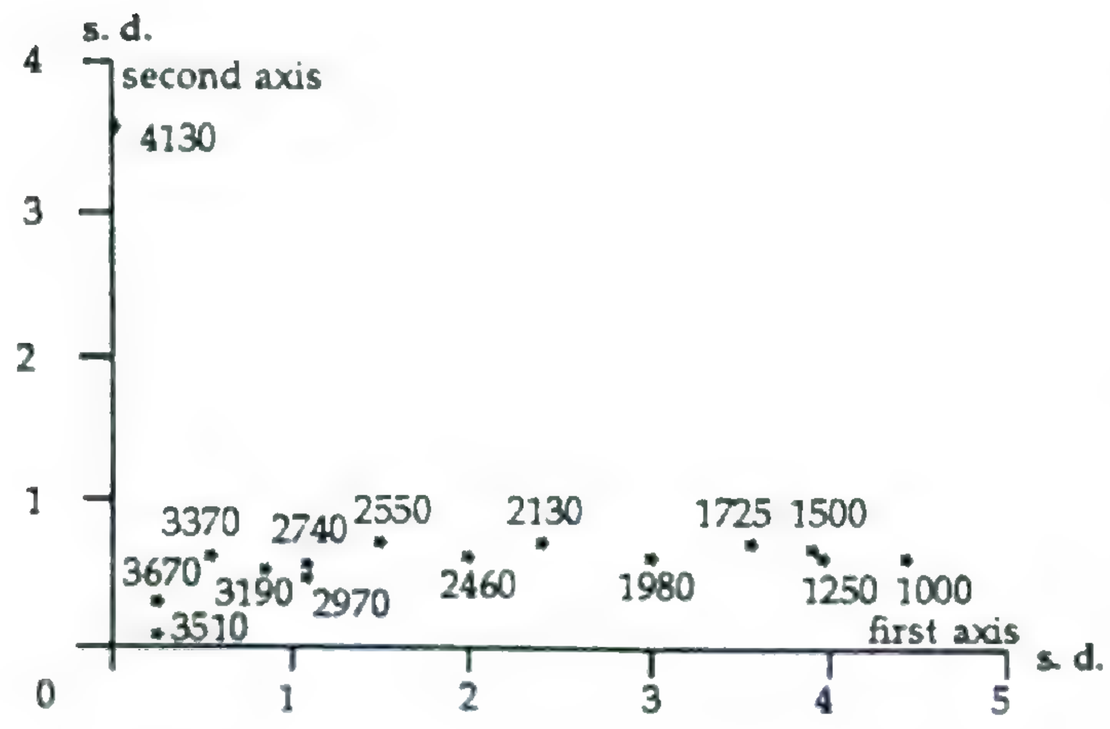



FIGURE 4. Distribution of sites over the first two axes generated by Detrended Correspondence Analysis; the scale of the axes are standard deviation units (s.d.). Eigenvalue first axis: 0.652; second axis: 0.259.

A log linear regression of these site similarities (%) against distance along the gradient permits the calculation of $CC_0$ at zero distance. In all cases regression was calculated using the first 5 points on the graph only. Beta diversity in half changes over an ecological distance of z intervals (in our case 1,000 m altitudinal difference) is then calculated as $\beta = (\log CC_0 - \log CC_z)/\log 2$. To evaluate differences in species turnover between lower and higher elevations, the altitudinal coenocline was divided into two sections. The lower part had the site at 1,250 m as reference stand and the higher part the site at 3,670 m.

## Results and Discussion

### CLIMATE

Day climate diagrams, following Ellenberg (1975) and including vapor pressure deficits, of the six stations along the transect (1,725–3,670 m) are based on hourly readings (Fig. 5). With increasing altitude, diurnal rhythms become less pronounced, a well-known pattern in equatorial montane forests (Walter, 1964), and a marked increase in humidity (hatched area) is notable above ca. 2,400 m as further shown by humidity conditions during daylight hours only (Fig. 6). Rainfall and humidity do not exhibit a linear relationship with altitude. Between about 2,000 m and 2,500 m there is a maximum in rainfall and a notable increase in humidity with altitude, which corresponds with the increase in slope of the transect (Fig. 1). Local wind circulation patterns may account for the observed humidity and rainfall pattern: in the early morning hours anabatic winds rise from the valley floor along the hillside and while rising, clouds may be formed through condensation, on a typical day resulting in precipitation during the early afternoon at an altitude of about 2,100 m (van der Weert et al., 1986). Accordingly, at higher altitudes sunshine was much rarer than in the valley and when it occurred it was during early morning hours and during late afternoons, when the clouds had passed onward (pers. obs.). During the night a drop in relative humidity, without an expected rise or even associated with a drop in temperature, was often observed (Fig. 7). This phenomenon, noted as far down the slope as 2,450 m and also known at the Sierra Nevada de Santa Marta, Colombia (van der Hammen, 1984), might be explained assuming the passing of a "dry" descending catabatic wind from the high (>5,000 m) snow-capped hinterlying volcanoes. These winds warm while descending, but apparently do not take up much moisture, perhaps due to the lack of bushy vegetation at higher elevations.

The distribution of tree base diffuse site factors (Anderson, 1964) with altitude shows that about 90–95% of the diffuse light is intercepted by the canopy (Fig. 8). Near the tree line at 3,670 m and at the *Polylepis*-dominated dwarf forest at 4,130 m the forest canopy is more open, with diffuse site factors of about 15% and 30%, respectively.

### BIOMASS PATTERNS

The biomass per unit surface area of the epiphytic tree crown subsamples (excluding phanerogams) varies considerably at a given altitude (Fig. 9A), but generally increases with altitude in agreement with quantitative measurements of bryophyte abundance in the forest understory along altitudinal gradients in Colombia (van Reenen & Gradstein, 1983) and Peru (Frahm, 1987c).

High bryophyte biomass values in the tropics have been attributed to rainfall above 100 mm per month (Pócs, 1980), and to foggy conditions (Grubb & Whitmore, 1966; Ellenberg, 1975). Frahm (1987c) observed a direct relationship between the biomass of epiphytic bryophytes in northeast Peru and the amount of radiation. The maximum recorded biomass value at a tree trunk by Frahm was 1.4 g/dm$^2$, while in this study the maximum bryophyte dry weight at the trunk base was 16 g/dm$^2$ (at 3,670 m). The climatic data presented from the Peruvian transect suggest that the local climate is notably drier than in our area, which predictably would result in lower bryophyte biomass values.

The rise in epiphytic biomass with altitude displays a marked increase around ca. 2,400 m that is not correlated with a sudden change in rainfall (Fig. 2), diffuse site factors (Fig. 8), or temperature (van de Weert et al., 1986), but coincides with an observed rapid increase of humidity above the 2,400 m mark (Figs. 5, 6). Ecophysiological research on bryophytes confirms the importance of moisture availability to bryophytic growth. Hosokawa et al. (1964) demonstrated for several epiphytic bryophytes a positive relationship between photosynthetic rate and relative humidity at equal light conditions. Because bryophyte photosynthesis is relatively insensitive to low temperatures (Dilks & Proctor, 1975), decreasing temperature should not negate the positive effects of high humidity on growth at higher elevations.

Long periods of high humidity not only allow for long periods of photosynthetic activity, but they also reduce the risk of desiccation. The latter factor

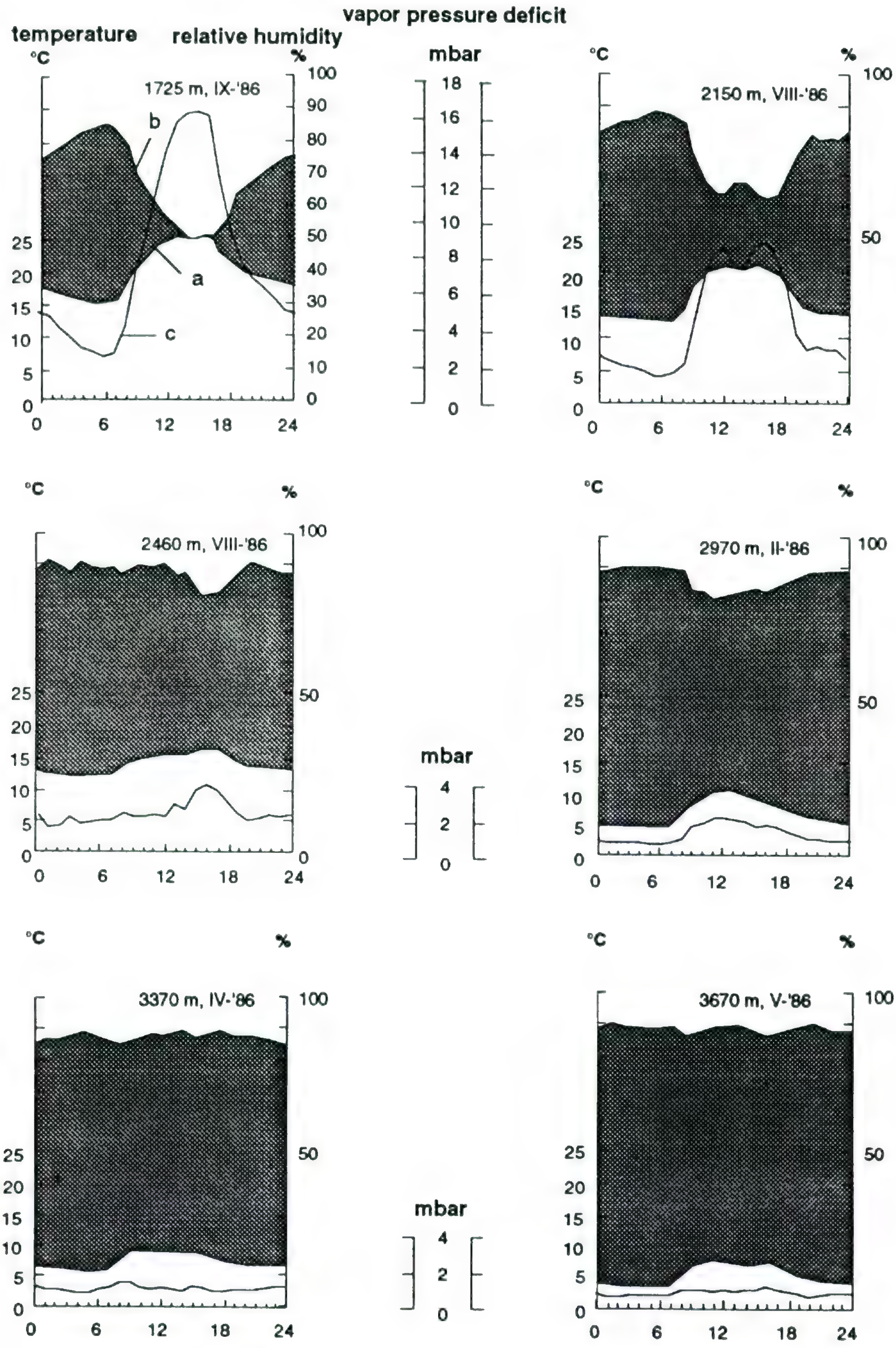
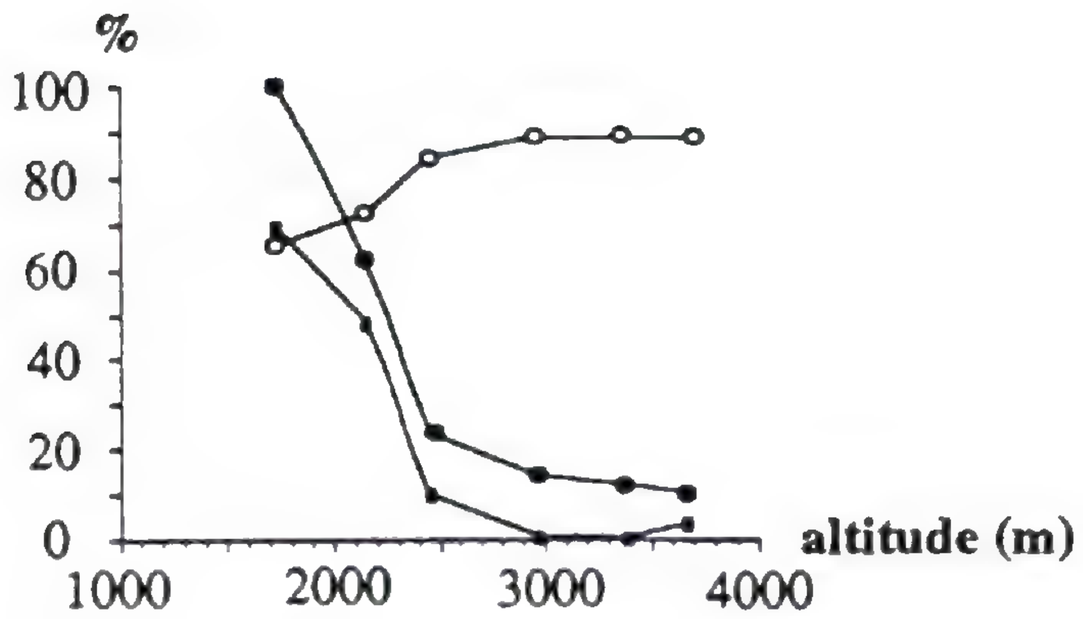



FIGURE 5. The daily course of temperature (a), relative humidity (b), and (derived) vapor pressure deficit (c) at different altitudes, based on hourly readings during 12 (1,725 m; 2,150 m; 2,460 m; 2,970 m) or 18 days (3,370 m; 3,670 m). Presentation following Ellenberg (1975).




- time (%) when the relative humidity is less than 70%
- mean vapor pressure deficit, expressed as a percentage of highest value (10.62 mbar)
- mean relative humidity (%)

FIGURE 6. Humidity conditions, as exemplified by three moisture indexes, in relation to altitude, based on hourly readings during daylight hours (06.00–18.00 hr.). Means of 12 (1,725 m; 2,150 m; 2,460 m; 2,970 m) or 18 days (3,370 m; 3,670 m).

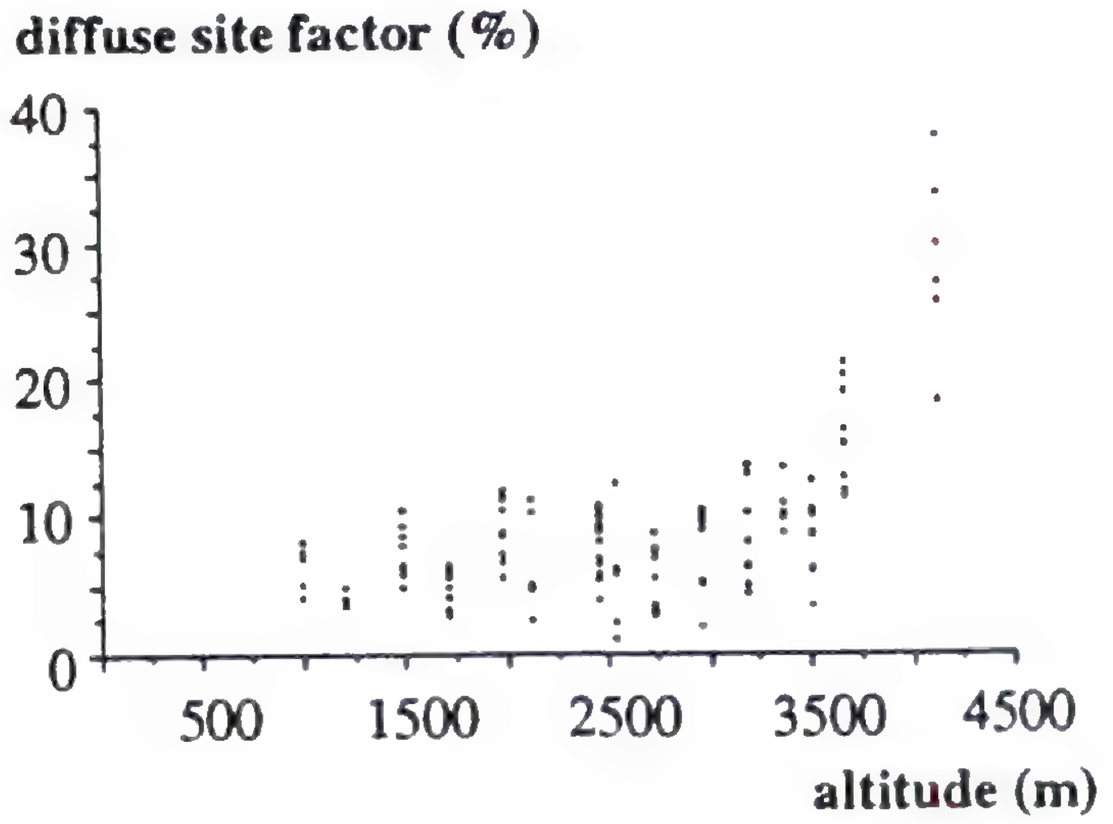



FIGURE 8. Mean percentage of diffuse light cut off by the canopy, expressed as diffuse site factors (Anderson, 1964) and calculated from hemispherical photographs taken at the bases of the investigated trees.

allows for the development of bryophyte growth forms that may attain a thick epiphytic layer (Fig. 9B) and hence a great biomass per surface area, such as tall turfs and pendents (Richards, 1984).

Another factor may be the greater life expectancy of the substrate. At higher elevations the productivity of the forest is lower (Grubb, 1977; Veneklaas, 1991) and therefore the trees are presumably older. $C^{14}$ analysis of the core wood at breast height of a 15-m-tall *Weinmannia mariquitae* Szyszyl. (Cunoniaceae) tree at 3,700 m altitude revealed a most probable age of 215 (±15) years (Hofstede et al., 1993).

Lichen biomass values were not determined separately from bryophytes, but were supposedly highest at altitudes below 2,500 m, due to the regular occurrence of large foliose growth forms, e.g., *Sticta* spp., at lower altitudes.

## EPIPHYTIC SPECIES NUMBERS

In total, 473 taxa (108 mosses, 187 liverworts, and 178 lichens) are recognized in the subsamples. Based on the amount of species grouping, these taxa are estimated to represent ca. 90% of the species present (with estimated species numbers of 113 for mosses, 220 for liverworts, and 198 for lichens, excluding an unknown number of crustose lichens).

Lichens may be subdivided into three main growth forms: foliose (110 taxa), fruticose (30 taxa), and crustose lichens (38 taxa). Crustose lichens include leprose (thallus powdery) and some squamulose (e.g., *Pannaria rubiginosa* (Ach.) Bory) forms. Fruticose lichens include filamentous (e.g., *Coenogonium* sp.) and loosely attached foliose growth forms with a thallus diameter of < 2 mm (e.g., *Everniastrum catawbiense* (Degel.) Hale). Squamulose growth forms are included with the foliose lichens, when the squamules regularly are

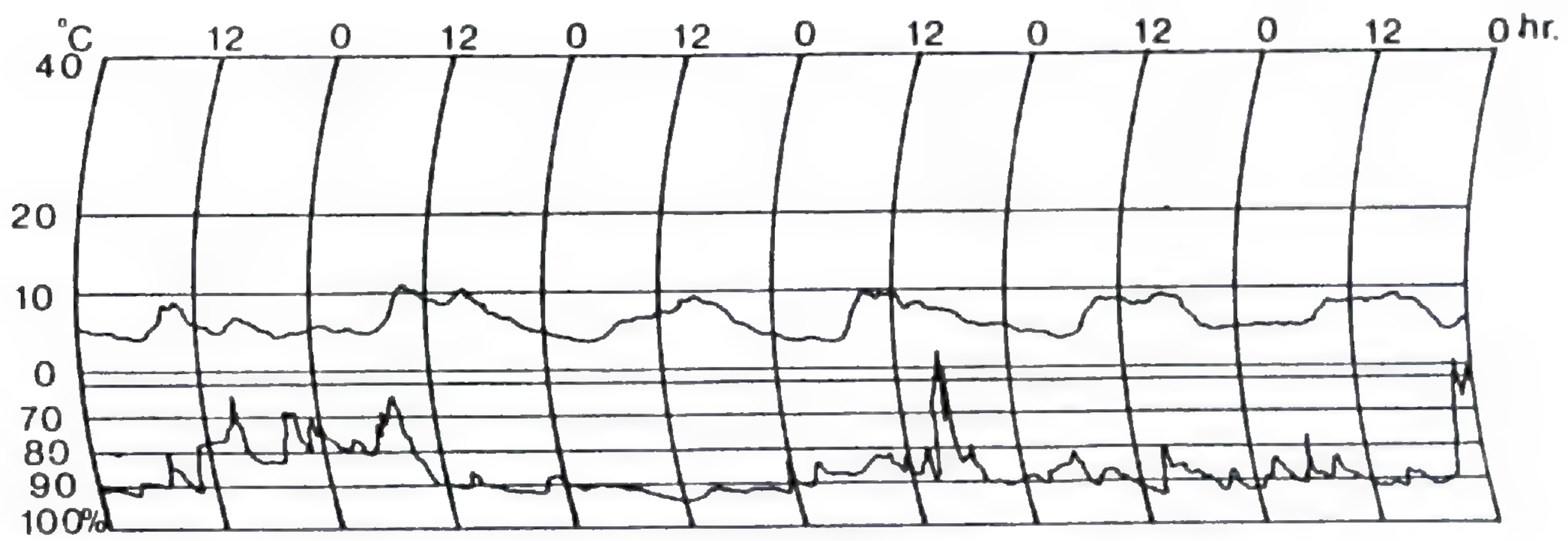



FIGURE 7. Thermohygrograph reading, TPN-transect, 9–15 May 1986, altitude 3,670 m.

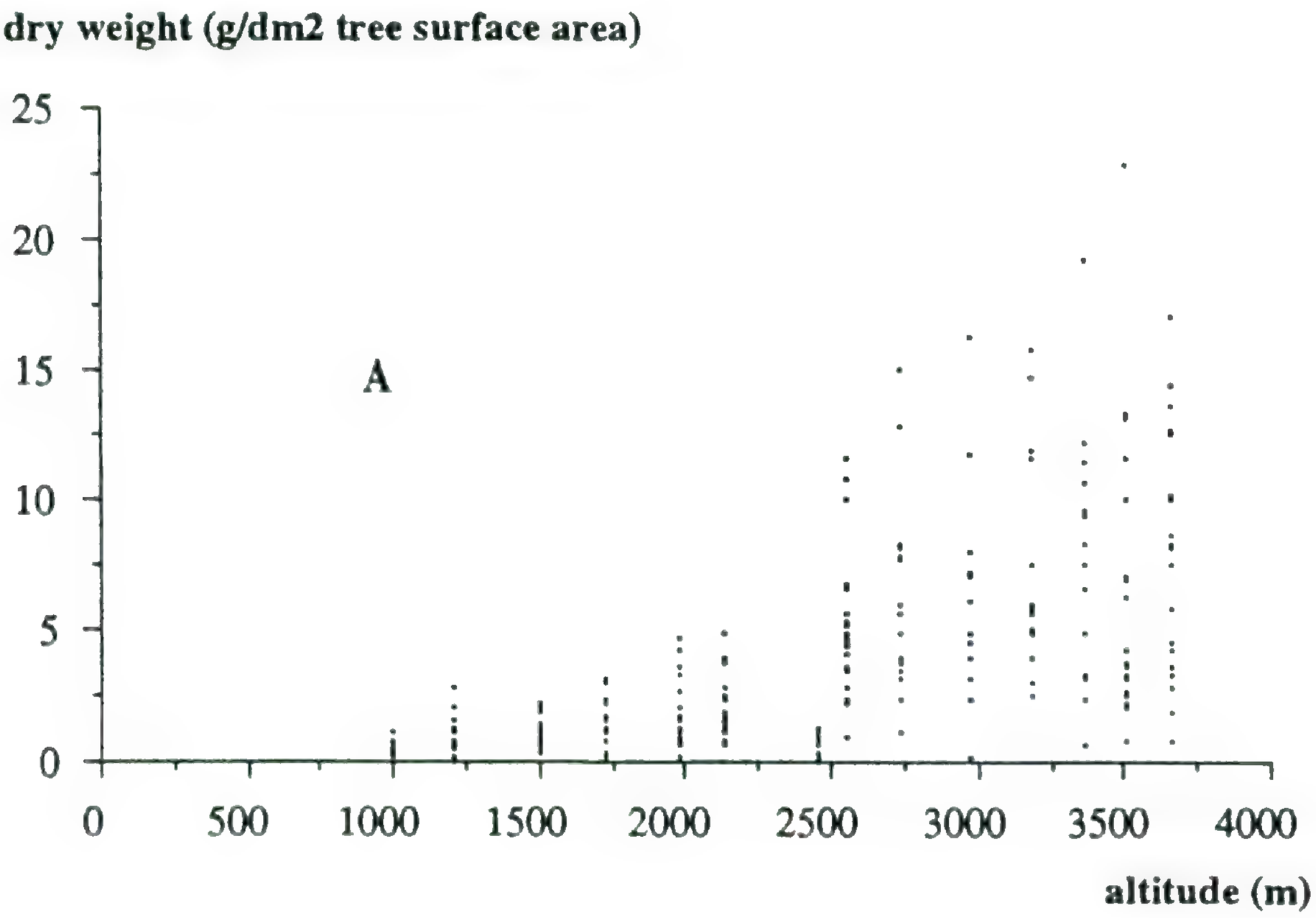



FIGURE 9. Biomass (A) and thickness (B) of the (living) epiphytic bryophyte layer. Each dot represents a subsample taken at the inner and middle parts of the branches within the canopy.

> 0.5 cm (e.g., *Normandina pulchella* (Borr.) Nyl.).

For many organisms the tropical region is richer in species than the temperate zone (e.g., Pianka, 1966). This may not apply to bryophytes and lichens, however. For example, recorded moss species numbers for the British Isles, Europe, the Guianas, and tropical America are, respectively, 700 (Smith, 1978), 1,084 (Corley et al., 1981), 234 (Florschütz-de Waard, 1991), and between 1,000 and 1,500 according to a rough estimation (Frahm & Gradstein, pers. comm.). Liverwort species numbers recorded for the same geographical areas are, respectively, 300 (Smith, 1990), 350 (Grolle, 1983), 375 (Gradstein & Hekking, 1989), and ca. 1,200 (Gradstein, 1988). Even though the number of bryophyte species in the tropics is likely to increase with continued exploration, it appears

TABLE 1. Epiphytic bryophyte and macrolichen richness in a temperate deciduous forest (Sweden), lowland tropical rainforest (Guianas), and montane tropical rainforest (Colombia): (1) from Sjögren (1961); (2) from Cornelissen & Ter Steege (1989); (3) from Montfoort & Ek (1990); (4) this study. Within the tropical areas sampling included the tree crown and in the Guianas epiphyllous species.

| | Number of trees sampled | Mosses | Liver-worts | Total bryophytes | Macro-lichens |
|---|---|---|---|---|---|
| Sweden; deciduous forest (1) | many | 78 | 17 | 95 | — |
| Guyana; dry evergreen *Eperua* spp. forest (2) | 11 | 28 | 53 | 81 | 33 |
| Guyana; mixed lowland rainforest (2) | 5 | 28 | 60 | 88 | 19 |
| French Guyana; mixed lowland rainforest (3) | 4 | 43 | 61 | 104 | 21 |
| Colombia; montane rainforest; 1,500 m (4) | 4 | 22 | 36 | 58 | 49 |
| Colombia; montane rainforest; 2,550 m (4) | 4 | 33 | 102 | 135 | 51 |
| Colombia; montane rainforest; 3,510 m (4) | 4 | 19 | 63 | 82 | 37 |

that temperate areas are richer in bryophytes (British Isles 1,000 species) than tropical lowland rainforest (Guianas 609 species). The higher relative contribution of liverworts to bryophyte species richness in the tropics (tropical America ca. 50%) than in temperate areas (Europe ca. 25%) is confirmed by data on epiphytic bryophyte diversity (Table 1). Total epiphytic bryophyte species numbers are similar in temperate Sweden, the tropical Guianas, and in Colombia, but species numbers in the tropics are likely to be higher due to the restrictive sampling methods used. Records on species numbers of lichens in the tropics are still incomplete. Sipman (1989) estimated lichen richness in the transect to be of the order of 600–900 species, compared to 1,355 recorded species for the British Isles (James, 1965).

Comparing bryophyte species numbers recorded on similar numbers of host trees in situations of near saturated species area curves (Table 1), at least for epiphytes no support is given for earlier assumptions (Richards, 1984, 1988) that wet montane tropical forests are richer in bryophyte species than tropical lowland rainforests (but epiphyllous species were not included in this study). Epiphytic macrolichen richness appears to be greater in tropical montane forest than in lowland forest.

In addition to limitations imposed by the restrictive sampling method by tree size, bark type, and location, bryophyte and lichen species numbers in general should be looked at with care for two reasons.

First, there is justification for treating epiphytic and terrestrial cryptogams separately, not only because epiphytic species are ecologically different, but also because, in particular in the lowland tropics, terrestrial sampling is likely to be biased. Tropical lowland forests have low cover percentages of terrestrial bryophytes, possibly partly due to the smothering effect of leaf litter and partly due to the combination of low light intensities and high temperatures (Richards, 1984; Frahm, 1987c). Species richness estimations of lowland areas are likely to be highly influenced by factors such as gaps, road banks, and fallen trees. Bias in sampling may largely be avoided by sampling of the epiphytic flora growing on trees within the forest only. Furthermore, terrestrial substrates are more likely to differ from each other structurally, chemically, and in terms of water availability than epiphytic sites, and thus habitat heterogeneity is more likely to cause noise in diversity patterns.

Second, epiphytic sampling should include systematic investigation of the forest canopy. In the lowland rainforest of the Guianas, over 50% of the epiphytic bryophyte species may be found exclusively in the canopy (Gradstein et al., 1990). Moreover, a more open forest may permit the descent of typical canopy species to the forest floor, confusing altitudinal species diversity patterns when only the forest floor is sampled. The reported rise in number of species of lichens (Sipman, 1989) and bryophytes (Gradstein et al., 1989) near the upper tree limit in the investigated transect, based on both terrestrial and epiphytic (0–3 m) sampling, can possibly be ascribed to the occurrence of canopy species near ground level, together with the influx of typical terrestrial páramo species.

## ALPHA DIVERSITY PATTERNS

The altitudinal distribution of 473 bryophyte and lichen taxa is presented in Table 2. Bryophyte and lichen richness patterns along the transect selected for study are not identical (Fig. 10). Whereas bryophyte richness shows a clear maximum between 2,550 m and 3,190 m, numbers of taxa of lichens decrease slightly between 1,500 m

TABLE 2. Recorded taxa and their distribution along the altitudinal transect. "X" = actual record; "•" = presumed occurrence; (# . . . refers to collection number).

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| Mosses | | | | | | | | | | | | | | | |
| *Aptychella proligera* (Broth.) Herzog | | | | | | | | X | X | X | | | | | |
| *Bartramia angustifolia* Mitt. | | | | | | | | | | | | | X | X | |
| *Bartramia* sp. A (# 123) | | | | | | X | | | | | | | | | |
| *Brachymenium consimile* (Mitt.) Jaeger | | | | | | X | | | | | | | | | |
| *Brachythecium* sp. A (# 168) | | | | | | X | | | | | | | | | |
| Bryaceae sp. A (# 1180) | | | | | | | | | | | | | | | X |
| *Bryum* sp. A | | X | | | | | | | | | | | | | |
| *Bryum* sp. B | | | X | X | X | | | | | | | | | | |
| Calymperaceae sp. A | | | | | X | | | | | | | | | | |
| *Calymperes afzelii* Sw. | X | | | | | | | | | | | | | | |
| *Calyptothecium duplicatum* (Schwaegr.) Broth. | | | | X | | | | | | | | | | | |
| *Campylium* ? sp. A | | | | | | | | | | | | | X | X | |
| *Campylopus fragilis* (Brid.) B.S.G./ *C. pittieri* Williams | | | | | | | | | X | X | X | X | X | X | X |
| *Campylopus reflexisetus* (C. Müll.) Broth. | | | | | X | • | • | X | X | • | X | X | X | | |
| *Campylopus* sp. A (# 1124) | | | | | X | X | | | | | | | | | |
| *Catagonium brevicaudatum* C. Müll. ex Broth. | | | | | | | | | | | | X | X | X | X |
| *Chorisodontium mittenii* (C. Müll.) Broth. | | | | | | | | X | X | • | X | X | X | X | X |
| *Ctenidium malacodes* Mitt. | | | X | • | X | X | • | • | • | X | | | | | |
| *Cyclodictyon rubrisetum* (Mitt.) Kuntze | | | | | | | X | X | • | • | X | X | | | |
| *Daltonia longifolia* Taylor | | | | X | X | X | X | X | X | X | X | X | X | X | X |
| *Dicranodontium meridionale* Bartram | | | | | | | | | | | | X | X | | |
| *Dicranoweisia* sp. A (# 969) | | | | | | | | | | | X | | | | |
| *Dicranum* cf. *paramicola* C. Müll. | | | | | | | | | X | | | | | | |
| *Entodon macropodus* (Hedw.) C. Müll. | | | | | X | | | | | | | | | | |
| *Erythrodontium longisetum* Hook. | X | X | X | X | X | | | | | | | | | | |
| *Eurynchium* sp. A (# 202) | | | | | X | X | | | | | | | | | |
| *Fissidens* spp. | | X | X | X | X | | • | • | X | • | X | | | | |
| *Groutiella apiculata* (Hook.) Crum & Steere | X | X | X | X | X | | | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Hypnella pilifera* (Hook. & Wilson) Jaeger | | | | | | | X | • | • | X | • | X | • | X | |
| *Hypopterygium tamariscinum* (Hedw.) Brid. | | | | X | X | X | X | | | | | | | | |
| *Isopterigium tenerum* (Sw.) Mitt. | X | • | • | X | • | X | X | X | | | | | | | |
| *Leiomela ecuadorensis* Robins. | | | | | | | | | | | | | X | X | |
| *Lepidopilum haplociliatum* (C. Müll.) Paris/*L. muelleri* (Hampe) Spruce | | | | | | X | X | • | X | X | | | | X | |
| *Lepidopilum* sp. A (# 610) | | | | | | | | | | X | | | | | |
| *Leptodontium capituligerum* C. Müll. | | | | | | | | | | | | | | | X |
| *Leptodontium* cf. *viticulosoides* (P.-Beauv.) Wijk & Margadant | | | | | | | | | | | | | | | X |
| *Leptodontium viticulosoides* var. *panamense* (Lorentz) Zander | | | | | | | | | X | • | X | | | | |
| *Leptodontium wallisii* (C. Müll.) Kindb. | | | | | | | | | | | | | | | X |
| *Leptotheca boliviana* Herzog | | | | | | | | | X | • | • | X | | | |
| *Lepyrodon tomentosus* (Hook.) Mitt. | | | | | | | | | | | X | • | • | • | X |
| *Leskeodon cubensis* (Mitt.) Thér. | | | | | | | | | X | • | • | • | X | | |
| *Leucobryum polakowskyi* (C. Müll.) Cardot | | | | | X | • | • | • | X | | | | | | |
| *Leucodontopsis geniculata* (Mitt.) Crum & Steere | X | X | X | X | | | | | | | | | | | |
| *Leucomium compressum* Mitt. | | X | • | X | | | | | | | | | | | |
| *Lindigia capillacea* (Hornsch.) Hampe | | | | | | X | | | | | | | | | |
| *Macromitrium cirrosum* (Hedw.) Brid. | | | | | | | | | | | | X | | | |
| *Macromitrium guatemalense* C. Müll./ *M. longifolium* (Hook.) Brid. | | | | | X | X | X | X | X | X | X | | | | |
| *Macromitrium portoricense* Williams | | | X | X | X | X | | | | | | | | | |
| *Macromitrium trachypodium* Mitt. | | | | | | | | | | | X | • | X | | |
| *Meteoridium remotifolium* (C. Müll.) Manuel | | | | X | X | X | • | X | | | | | | | |
| *Mittenothamnium reptans* (Hedw.) Cardot | | | | X | X | X | X | X | X | X | • | X | | | |
| *Neckera chilensis* Schimp. ex Mont. | | | | | | | | | | | | | | X | |
| *Neckera scabridens* C. Müll. | | | | | | X | | | | | | | | | |
| *Neckeropsis undulata* (Hedw.) Reichardt | | | | X | X | | | | | | | | | | |
| *Orthostichopsis tetragona* (Hedw.) Broth. | | X | | | | | | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Palamocladium leskeoides* (Hook.) E. G. Britt. | | | X | • | X | | | | | | | | | | |
| *Papillaria nigrescens* (Hedw.) Jaeger | X | X | X | X | X | | | | | | | | | | |
| *Phyllogonium fulgens* (Hedw.) Brid. | | | | | X | X | X | X | X | • | X | | | | |
| *Pilotrichella flexilis* (Hedw.) Ångstr. | | | X | • | • | X | | | | | | | | | |
| *Pireella fendleri* (C. Müll.) Card. | X | • | X | | | | | | | | | | | | |
| *Pireella cavifolia* (Card. & Herz.) Card. | | | | X | X | • | • | X | | | | | | | |
| *Plagiomnium rhynchophorum* (Hook.) T. J. Kop. | | | | | | X | X | • | • | X | | | | | |
| *Plagiothecium novo-granatense* (Hampe) Mitt. | | | | | | | | X | • | X | X | X | X | X | |
| *Porothamnium* aff. *comosum* | | | | | | | | | | | X | X | X | | |
| *Porotrichodendron superbum* (Taylor) Broth. | | | | | | | | X | X | • | • | X | X | X | X |
| *Porotrichum* spp. | | X | • | X | X | X | X | X | X | X | X | | | | |
| *Prionodon densus* (Hedw.) C. Müll. var. *densus* | | | | X | X | X | • | X | | | | | | | |
| *Prionodon densus* (Hedw.) C. Müll. var. *luteo-virens* (Taylor) Bartr. | | | | | | | X | X | X | X | X | | | | |
| *Prionodon fusco-lutescens* Hampe | | | | | | | X | X | X | X | X | X | X | X | |
| *Pterobryon densum* Hornsch. | | | | | X | | | | | | | | | | |
| *Pyrrhobryum mnioides* (Hook.) Manuel | | | | | | | | | | | X | X | X | X | |
| *Pyrrhobryum spiniforme* (Hedw.) Mitt. | | | | | | | | X | | | | | | | |
| *Racopilum tomentosum* (Hedw.) Brid. | | | | | | X | • | • | • | X | | | | | |
| *Rhegmatodon polycarpus* (Griff.) Mitt. | | | | X | X | | | | | | | | | | |
| *Rhizogonium lindigii* (Hampe) Mitt. | | | | | | | | | X | • | • | • | X | | |
| *Rhodobryum grandifolium* (Taylor) C. Müll. | | | | | | | | | | | | | | | X |
| *Rhynchostegiopsis* cf. *flexuosa* (Sull.) C. Müll. | | | | | | | | | | | | X | | | |
| *Rhynchostegiopsis tunguraguana* (Mitt.) Broth. | | | | | | | | | | | X | | | | |
| *Schlotheimia angustifolia* Mitt. | | X | X | X | X | X | | | | | | | | | |
| *Schoenobryum gardneri* Mitt. | X | X | • | • | X | X | | | | | | | | | |
| *Sematophyllum cuspidiferum* Mitt. | | | | | | X | X | X | X | • | X | | | | |
| *Sematophyllum flavidum* Mitt. | | | | | | | X | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Sematophyllum insularum* (Sull.) Mitt./ *S. napoanum* (De Not.) Steere | | | | | | | X | X | X | X | X | X | X | X | |
| *Sematophyllum subpinnatum* (Brid.) Britt. | X | X | X | X | X | X | X | | | | | | | | |
| Splachnaceae sp. A (# 603) | | | | | | | | | | X | | | | | |
| *Squamidium leucotrichum* (Taylor) Broth. | | | | | | | | X | X | X | X | X | | | |
| *Squamidium livens* (Schwaegr.) Broth. | | | | X | | | | | | | | | | | |
| *Squamidium nigricans* (Hook.) Broth. | | X | • | X | X | X | • | X | | | | | | | |
| *Stenodictyon wrightii* (Sull. & Lesq.) Crosby | | | | | | | | X | • | X | • | X | X | X | |
| *Streptopogon calymperes* C. Müll. ex Geh. | | | | X | X | X | | | | | | | | | |
| *Streptopogon erythrodontus* (Taylor) Wilson | | | | | | X | | | | | | | | | |
| *Syrrhopodon* cf. *elongatus* Sull. | | | | | | | | X | | | | | | | |
| *Syrrhopodon gaudichandii* Mont. | | | | | X | | | | | | | | | | |
| *Syrrhopodon incompletus* Schwaegr. s. lat. | | | | X | | | | | | | | | | | |
| *Syrrhopodon lycopodioides* (Brid.) C. Müll. | | | | | | | | | X | | | | | | |
| *Syrrhopodon parasiticus* (Brid.) Besch. | | X | X | X | | | | | | | | | | | |
| *Thamnobryum* sp. A (# 1075) | | | | | X | | | | | | | | | | |
| *Thuidium antillarum* Besch. | | | X | X | X | • | • | X | | | | | | | |
| *Thuidium delicatulum* (Hedw.) B.S.G. var. *peruvianum* (Mitt.) Crum | | | | | | | | | | X | X | | | | |
| *Thuidium minutulum* (Hedw.) B.S.G. | | | | | X | X | • | • | • | X | | | | | |
| *Tortula andicola* Mont. | | | | | | | | | | | | | | | X |
| *Trachyxiphium* cf. *subfalcatum* (Hampe) Buck | | | | | X | | | | | | | | | | |
| *Zelometeorium patulum* (Hedw.) Manuel | | | | | X | | | | | | | | | | |
| *Zygodon* cf. *peruvianus* Sull. | | | | | | X | • | X | X | X | X | X | | | |
| *Zygodon fragilis* Robins. | | | | | | | | | | | | | | | X |
| *Zygodon pichinchensis* (Taylor) Mitt. | | | | | | | | | | | | | | | X |
| *Zygodon reinwardtii* (Hornsch.) Braun | | | | | X | X | X | X | X | • | X | | | | |
| *Zygodon squarrosus* (Taylor) C. Müll. | | | | | | | | | | | | | X | X | |
| Liverworts | | | | | | | | | | | | | | | |
| *Acanthocoleus aberrans* (Lindenb. & Gott.) Kruijt | | | | X | X | X | X | X | | | | | | | |
| *Adelanthus crossii* Spruce | | | | | | | | | X | • | • | • | • | X | |
| *Adelanthus decipiens* (Hook.) Mitt. | | | | | | | | X | X | X | X | X | | | |
| *Adelanthus lindenbergianus* (Lehm.) Mitt. | | | | | | | | | | | | X | X | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Adelanthus pittieri* (Steph.) Grolle | | | | | | | | X | X | X | X | X | X | X | |
| *Amphilejeunea viridissima* Schust. | | | | | | X | X | X | X | X | X | | | | |
| *Anastrophyllum auritum* (Lehm.) Steph. | | | | | | | | | | | X | X | X | X | X |
| *Anastrophyllum leucocephalum* (Taylor) Steph. | | | | | | | | | | | X | • | X | X | |
| *Anastrophyllum piligerum* (Nees) Steph. | | | | | | | | | X | | | | | | |
| *Anastrophyllum tubulosum* (Nees) Grolle | | | | | | | | | | | | | X | X | |
| *Aneura* spp. | | | | | | | | X | X | X | X | X | | | |
| *Anoplolejeunea conferta* (Meissn.) Steph. | | X | X | X | X | • | X | X | X | X | X | X | X | X | |
| *Aureolejeunea fulva* Schust. | | | | | | | X | X | X | X | X | | | | |
| *Aureolejeunea paramicola* (Herz.) Schust. | | | | | | | | | | X | X | X | X | X | |
| *Bazzania* aff. *chilensis* (Steph.) Fulford | | | | | | | | | | | X | | | | |
| *Bazzania breuteliana* (Lindenb. & Gott.) Trevis. | | | | | | | | X | X | X | X | X | X | | |
| *Bazzania hookeri* (Lindenb.) Trevis. | | | | | | | X | X | X | X | X | X | X | X | |
| *Bazzania longistipula* (Lindenb.) Trevis. | | | | | | | | X | X | X | X | X | X | | |
| *Blepharolejeunea incongrua* (Lindenb. & Gott.) van Slag. & Kruijt | | | | | | X | X | • | X | X | X | • | X | | |
| *Blepharolejeunea securifolia* (Steph.) Schust. | | | | | | | X | X | • | X | • | • | • | X | X |
| *Blepharostoma trichophylla* (L.) Dum. | | | | | | | | | | | | | X | X | |
| *Brachiolejeunea laxifolia* (Taylor) Schiffn. | | | | X | X | X | X | X | X | X | X | | | | |
| *Brachiolejeunea leiboldiana* (Gott. & Lindenb.) Schiffn. | | | | X | | | | | | | | | | | |
| *Brachiolejeunea phyllorhiza* (Nees) Kruijt & Gradst. | X | X | | | | | | | | | | | | | |
| *Bryopteris diffusa* (Sw.) Nees | X | X | | | | | | | | | | | | | |
| *Bryopteris filicina* (Sw.) Nees | | X | X | X | X | | | | | | | | | | |
| *Calypogeia cyclostipa* (Spruce) Steph. | | | | | | | X | • | X | X | • | X | | | |
| *Calypogeia peruviana* Nees & Mont. | | | | | | | X | X | X | X | X | X | X | X | |
| *Cephalozia bischlerae* Fulford | | | | | | | | | | | | | X | | |
| *Cephalozia crassifolia* (Lindenb. & Gott.) Fulford | | | | | | | | X | X | X | • | X | | | |
| *Ceratolejeunea* cf. *maritima* (Spruce) Steph. | | X | X | X | X | • | X | X | | | | | | | |
| *Ceratolejeunea grandiloba* Jack. & Steph. | | | | | | X | • | X | X | X | | | | | |
| *Ceratolejeunea patentissima* (Hampe & Gott.) Evans | | | | | | | | | X | | | | | | |
| *Ceratolejeunea* sp. A | | X | X | | | | | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Cheilolejeunea choachina* (Gott.) Grolle | | X | X | X | X | X | X | • | X | X | | | | | |
| *Cheilolejeunea rigidula* (Nees & Mont.) Schust. | X | X | X | X | X | | | | | | | | | | |
| *Cheilolejeunea* spp. | | | | | | | | X | • | • | X | X | X | X | |
| *Cheilolejeunea trifaria* (Reinw. et al.) Mizut. | X | X | X | X | X | | | | | | | | | | |
| *Colura naumannii* (Schiffn.) Steph. | | | | | | | | X | • | • | • | X | X | | |
| *Colura tenuicornis* Steph. | | | | | X | • | X | X | X | • | X | • | X | X | |
| *Cyclolejeunea accedens* (Gott.) Evans | | | | | | | | | X | • | X | | | | |
| *Cyrtolejeunea holostipa* (Spruce) Evans | | | X | • | • | • | • | X | X | • | X | | | | |
| *Cyrtolejeunea* sp. A | | | | | | | | | X | X | | | | | |
| *Dicranolejeunea axillaris* (Nees & Mont.) Schiffn. | | | | | | X | X | | | | | | | | |
| *Diplasiolejeunea pauckertii* (Nees) Steph. | | | | | X | • | X | X | X | X | X | X | X | X | X |
| *Drepanolejeunea andina* Herzog | | | | | | | | | | | | X | X | X | X |
| *Drepanolejeunea inchoata* (Meissn.) Steph. | | | | | X | X | X | X | X | X | | | | | |
| *Drepanolejeunea* spp. | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| *Frullania apiculata* (Reinw. et al.) Nees | | | | | X | • | • | X | X | X | X | | | | |
| *Frullania arecae* (Spreng.) Gott. | | X | • | X | X | X | X | X | | | | | | | |
| *Frullania brasiliensis* Raddi | | X | X | X | X | X | X | X | X | X | X | X | | | |
| *Frullania caulisegua* (Nees) Nees | | X | X | X | X | • | • | X | X | • | X | | | | |
| *Frullania* cf. *moritziana* Lindenb. & Gott. | | | | | | | | | | X | | | | | |
| *Frullania* cf. *paradoxa* Lehm. & Lindenb. | | | | | | | | | | X | • | X | X | X | |
| *Fullania convoluta* Lindenb. & Hampe | | | | | | | | X | • | X | X | X | X | X | |
| *Frullania ecuadorensis* Steph. | | X | | | | | | | | | | | | | |
| *Frullania ericoides* (Nees) Mont. | X | X | X | X | | | | | | | | | | | |
| *Frullania peruviana* Gott. | | | | | | | | X | X | • | • | X | X | X | |
| *Frullania pittieri* Steph. | | | X | • | • | • | X | | | | | | | | |
| *Frullania riojaneirensis* (Raddi) Ångstr. | X | X | X | X | X | X | X | • | • | X | | | | | |
| *Frullania sphaerocephala* Spruce | | | | | | | | | | X | • | • | • | X | |
| *Frullania standaertii* Steph. | | | | X | X | X | • | X | • | • | X | | | | |
| *Frullania tetraptera* Nees & Mont. | | | | | | | | | X | X | X | X | • | X | X |
| *Frullania winteri* Steph. | | | | X | X | | | | | | | | | | |
| *Frullanoides densifolia* Raddi | X | • | X | X | X | X | X | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Frullanoides liebmanniana* (Lindenb. & Gott.) van Slag. | X | X | | | | | | | | | | | | | |
| *Harpalejeunea ancistrodes* (Spruce) Schiffn. | | | | | | | X | X | • | X | X | X | X | X | X |
| *Harpalejeunea* cf. *oxyphylla* (Nees & Mont.) Steph. | | | | | | | | X | | | | | | | |
| *Herbertus acanthelius* Spruce | | | | | | | | X | • | • | X | X | • | X | |
| *Herbertus colombianus* Van Reenen | | | | | | | | | | | | | | X | |
| *Herbertus juniperoideus* (Sw.) Grolle | | | | | | | | X | X | X | X | X | X | | |
| *Herbertus pensilis* (Taylor) Spruce | | | | | | | | | X | X | X | X | X | X | |
| *Herbertus subdentatus* (Steph.) Fulford | | | | | | | | | | | | X | X | X | |
| *Heteroscyphus polyblepharis* (Spruce) Schiffn. | | | | | | | X | X | • | X | X | • | • | X | |
| *Jamesoniella rubricaulis* (Nees) Grolle s. lat. | | | | | | | | X | X | • | X | X | X | X | |
| *Kurzia flagellifera* (Steph.) Grolle | | | | | | | | | X | | | | | | |
| *Lejeunea* aff. *ambigua* Lindenb. & Gott. | | | | | | | | | | X | | | | | |
| *Lejeunea flava* (Sw.) Nees | | | | X | X | X | X | X | | | | | | | |
| *Lejeunea laetevirens* Nees & Mont. | X | X | X | X | X | X | X | | | | | | | | |
| *Lejeunea megalantha* Spruce | | | | | | X | X | • | X | | | | | | |
| *Lejeunea reflexistipula* (Lehm. & Lindenb.) Steph. | | | | | | X | X | X | X | X | | | | | |
| *Lejeunea* sp. A (# 572) | | | | X | X | X | X | X | X | X | X | | | | |
| *Lejeunea* sp. B (# 561) | | | | | X | • | X | X | X | X | X | | | | |
| Lejeuneaceae | X | X | X | X | X | X | X | X | X | X | X | • | X | | |
| *Lepicolea pruinosa* (Taylor) Spruce | | | | | | | | X | X | X | X | X | X | X | |
| *Lepidolejeunea involuta* (Gott.) Grolle | | X | X | X | • | • | X | • | • | X | | | | | |
| *Lepidolejeunea spongia* (Spruce) Thiers | | | | | | | X | X | • | X | X | • | X | | |
| *Lepidozia* spp. | | | | | X | • | • | X | X | X | X | X | X | X | |
| *Leptolejeunea elliptica* (Lehm. & Lindenb.) Schiffn. | | | | | | | | | X | | | | | | |
| *Leptoscyphus amphibolius* (Nees) Grolle | | | | | | | | X | X | | | | | | |
| *Leptoscyphus cuneifolius* (Hook.) Mitt. | | | | | | | | X | X | X | X | X | X | X | X |
| *Leptoscyphus jackii* (Steph.) Grolle | | | | | | | | | X | X | • | X | X | X | |
| *Leptoscyphus physocalyx* (Hampe & Gott.) Gott. | | | | | | | | | | X | | | | | |
| *Leptoscyphus porphyrius* (Nees) Grolle | | | | | X | • | • | • | X | X | X | X | X | X | |
| *Lindigianthus cipaconeus* (Gott.) Kruijt & Gradst. | | | | | | | | X | • | X | X | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Lophocolea* aff. *connata* (Sw.) Nees | | | | | | | X | • | X | X | • | X | | | |
| *Lophocolea bidentata* (L.) Dum. | | | | | | X | X | X | • | • | X | X | | | |
| *Lophocolea muricata* (Lehm.) Nees | | | | X | • | • | X | X | • | • | X | | | | |
| *Lophocolea quadridentata* Spruce | | | | | | | | | X | • | X | X | X | X | |
| *Lophocolea trapezoidea* Mont. | | | | | | | X | X | X | X | X | X | X | X | |
| *Lopholejeunea subfusca* (Nees) Schiffn. | | X | X | | | | | | | | | | | | |
| *Marchesinia brachiata* (Sw.) Schiffn. | | | X | X | X | X | • | X | | | | | | | |
| *Marchesinia robusta* (Mitt.) Schiffn. | | | X | | | | | | | | | | | | |
| *Mastigolejeunea auriculata* (Wilson) Schiffn. | X | • | X | | | | | | | | | | | | |
| *Metzgeria decipiens* (Mass.) Schiffn. | | | | X | X | X | X | X | X | X | X | X | X | X | X |
| *Metzgeria fruticola* Spruce | | | | | X | X | • | X | | | | | | | |
| *Metzgeria leptoneura* Spruce | | | | | | | X | X | | | | | | | |
| *Metzgeria metaensis* Kuw. | | | | | | | | | | | | | | | X |
| *Metzgeria* spp. (sect. *Metzgeria*) | X | X | X | X | X | X | • | X | | | | | | | |
| *Microlejeunea* spp. | | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| *Monoclea gottschei* Lindb. | | | | | | X | X | X | X | X | X | | | | |
| *Odontolejeunea lunulata* (Web.) Schiffn. | | | | | X | X | | | | | | | | | |
| *Omphalanthus filiformis* (Sw.) Nees/ *O. platycoleus* Herzog | | | | X | X | X | X | X | X | X | X | | | | |
| *Omphalanthus ovalis* (Lindenb. & Gott.) Gradst. | | | | | | X | X | • | X | X | | | | | |
| *Plagiochila adiantoides* (Sw.) Dum. | | | | | | | | X | • | X | X | | | | |
| *Plagiochila alpina* Gott. | | | | | | | | X | • | X | | | | | |
| *Plagiochila bancroftii* Steph. | X | X | X | X | X | • | X | | | | | | | | |
| *Plagiochila beskeana* Steph. | X | • | • | X | | | | | | | | | | | |
| *Plagiochila bidens* Gott. | | | | | | | X | X | X | X | X | • | X | | |
| *Plagiochila bogotensis* Gott. | | | | | | | | X | X | | | | | | |
| *Plagiochila bursata* (Desv.) Lindenb. | | | | X | • | X | X | X | X | X | X | | | | |
| *Plagiochila choachina* Gott. | | | | X | X | X | X | • | X | X | | | | | |
| *Plagiochila corniculata* Dum. | | | | | X | X | X | X | X | X | X | X | X | | |
| *Plagiochila densispina* Steph. | | | | | | X | X | | | | | | | | |
| *Plagiochila disticha* (Lehm. & Lindenb.) Mont. | | | | | | X | | | | | | | | | |
| *Plagiochila divaricata* Lindenb. | | | | | | | | X | • | • | X | | | | |
| *Plagiochila diversifolia* Lindenb. & Gott. | | | | | | X | | | | | | | | | |
| *Plagiochila diversispina* Taylor | | | | | | X | X | • | X | X | X | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Plagiochila domincensis* Taylor | | | | | | | | X | | | | | | | |
| *Plagiochila echinella* Gott. | | | | | | | | X | X | X | X | X | X | X | |
| *Plagiochila esmeraldana* Steph. | | | | | | | X | X | X | X | X | | | | |
| *Plagiochila falcata* Steph. | | | X | | | | | | | | | | | | |
| *Plagiochila fragilis* Taylor | | | | X | X | X | | | | | | | | | |
| *Plagiochila fuscolutea* Taylor | | | | | | | | | | | X | X | X | X | |
| *Plagiochila guilleminiana* Mont. | | X | • | X | • | X | X | | | | | | | | |
| *Plagiochila hansmeyeri* Steph. | | | | | | X | • | • | X | X | X | X | X | X | |
| *Plagiochila jamesonii* (Willd.) Lindenb. | | X | | | | | | | | | | | | | |
| *Plagiochila laetevirens* Lindenb. | | | | | | X | • | • | • | X | | | | | |
| *Plagiochila macrifolia* Taylor | | | | | | X | X | • | X | | | | | | |
| *Plagiochila micropterys* Gott. | | | | | | X | | | | | | | | | |
| *Plagiochila paludosa* Steph. | | | | | | | | X | X | | | | | | |
| *Plagiochila rutilans* Lindenb. | | | | | | | | X | X | X | X | | | | |
| *Plagiochila* sp. A (# 1164) | | | | | | | | | | | | | | | X |
| *Plagiochila* sp. B (# 1354) | | | | | | | | | | | | | | X | |
| *Plagiochila* sp. C (# 1367) | | | | | | | | | | | | | X | | |
| *Plagiochila* sp. D (# 1372) | | | | | | | | | | | X | | | | |
| *Plagiochila* sp. E (# 121) | | | | | | X | | | | | | | | | |
| *Plagiochila* sp. F (# 1392) | | | X | X | | | | | | | | | | | |
| *Plagiochila subplana* Lindenb. | | X | X | X | X | X | X | | | | | | | | |
| *Plagiochila superba* Lindenb. | | | | | | | | X | • | X | | | | | |
| *Plagiochila sylvicultrix* Spruce | | | | | | | | X | X | | | | | | |
| *Porella brasiliensis* (Raddi) Schiffn. | X | • | X | | | | | | | | | | | | |
| *Porella crispata* (Hook.) Trev. | | X | X | | | | | | | | | | | | |
| *Porella swartziana* (Web.) Trev. | | X | | | | | | | | | | | | | |
| *Prionolejeunea* cf. *aemula* (Gott.) Evans | | | | | | X | X | • | • | X | X | | | | |
| *Prionolejeunea* sp. A (# 614) | | | | | | X | • | • | • | X | | | | | |
| *Prionolejeunea* spp. | | | | | | X | X | X | X | X | X | X | | | |
| *Radula caldana* Ångst. | X | X | | | | | | | | | | | | | |
| *Radula mollis* Lindenb. et Gott. | | X | X | X | X | X | | | | | | | | | |
| *Radula nudicaulis* Steph. | | | | | | | | | | | X | | | | |
| *Radula plumosa* Mitt. ex Steph. | | | | | | X | X | X | | | | | | | |
| *Radula sinuata* Gott. ex Steph. | | | | X | X | | | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Radula sonsonensis* Steph. | | | | | | | | X | X | X | X | | | | |
| *Radula tectiloba* Steph. | X | | | | | | | | | | | | | | |
| *Radula tenera* Mitt. ex Steph. | | | | | | | | | | X | X | X | X | | |
| *Radula voluta* Taylor | | | | | | X | X | X | • | • | X | • | • | • | X |
| *Riccardia aberrans* (Steph.) Gradst. | | | | | | | | | | X | X | X | X | X | |
| *Riccardia andina* (Spruce) Herz. | | | | | | | | X | X | X | • | X | | | |
| *Riccardia capillacea* (Steph.) Meenks & De Jong var. *capillacea* | | | | | | | | | | X | • | X | X | X | |
| *Riccardia ciliolata* (Spruce) Gradst. | | | | | | | | | | | | X | X | X | |
| *Riccardia* spp. | | | | | | X | X | X | • | X | X | X | X | X | |
| *Scapania portoricensis* Hampe & Gott. | | | | | | | | | X | X | X | X | X | X | |
| *Schiffneriolejeunea polycarpa* (Nees) Gradst. | | X | X | | | | | | | | | | | | |
| *Symbieizidium barbiflorum* (Lindenb. & Gott.) Evans | | X | X | X | | | | | | | | | | | |
| *Symphyogyna brasiliensis* Nees | | | | | | | | | | | | | X | X | |
| *Symphyogyna brongniartii* Mont. | | | | | | X | X | X | X | X | X | • | X | | |
| *Symphyogyna marginata* Steph. | | | | | | | | | X | X | | | | | |
| *Syzygiella integerrima* Steph. | | | | | | | | | | X | • | • | X | | |
| *Syzygiella perfoliata* (Swartz) Spruce | | | | | | | | X | X | | | | | | |
| *Taxilejeunea lancifolia* Steph. | | | | | | X | X | X | | | | | | | |
| *Taxilejeunea pallescens* (Mitt.) Steph. | | | | | | | | | X | X | • | • | X | | |
| *Taxilejeunea pterigonia* (Lehm. & Lindenb.) Schiffn. | | | | | | X | X | X | X | X | X | | | | |
| *Taxilejeunea sulphura* (Lehm. & Lindenb.) Schiffn. | | | | | | | X | • | • | X | | | | | |
| *Telaranea nematodes* (Gott. ex Aust.) Howe | | | | | X | • | X | X | X | X | X | • | X | | |
| *Trachylejeunea domincencis* Steph. | | | | | | | | | | X | X | • | X | X | |
| *Trichocolea tomentosa* (Sw.) Gott. | | | | | | X | X | X | X | X | X | X | X | X | |
| Crustose lichens | | | | | | | | | | | | | | | |
| *Agonimia* sp. A (# 266) | | X | X | | | | | | | | | | | | |
| *Anthracothecium* sp. A (# 1237) | X | X | X | | | | | | | | | | | | |
| *Astrothelium* ? sp. A (# 1210) | | | X | | | | | | | | | | | | |
| *Bacidia* sp. A (# 413) | X | | | | | | | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Bacidia* spp. | | | | | | X | X | • | • | • | X | • | • | X | |
| *Buellia modesta* (Krempelh.) Müll. Arg. | X | X | X | X | X | • | • | X | • | X | • | X | | | |
| *Caloplaca brebissonii* (Fée) Haffeln. & Poelt | | | | | X | X | • | X | • | • | X | | | | |
| *Chiodecton rubricinctum* (Ehrenb.) Nyl. | X | X | X | X | X | | | | | | | | | | |
| *Chiodecton* sp. A (# 687) | | | | | | | | | | X | X | | | | |
| *Chiodecton* spp. | X | X | X | X | X | X | • | X | • | X | X | X | | | |
| *Cryptothecia* spp. | | X | X | X | | | | | | | | | | | |
| *Dictyonema sericeum* (Sw.) Berk. | | | | | | X | • | • | X | | | | | | |
| *Dictyonema* sp. A (# 1008) | | | | | | | | | | | X | | | | |
| *Dictyonema* spp. | | | | X | • | • | • | X | • | • | X | X | | | |
| *Dimerella* spp. | | | X | X | X | X | X | X | • | X | • | X | X | • | X |
| Graphidaceae | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| *Haematomma puniceum* (Ach.) Massal. | | | X | X | | | | | | | | | | | |
| *Hastifera* sp. | | | | | | | | | | | X | • | X | X | |
| indet (sterile crustose lichen) | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| *Lecania sulphureofusca* (Fée) Müll. Arg. | | | | | | | | | | X | | | | | |
| *Lecanora* spp. | X | • | X | X | • | • | • | • | X | | | | | | |
| *Lecidea piperis* Spreng. | | | X | X | X | • | X | | | | | | | | |
| *Lecidea russula* Ach. | | | X | X | | | | | | | | | | | |
| *Lecidea* sp. A (# 355) | X | X | X | | | | | | | | | | | | |
| *Lecidea* sp. B (# 805) | | | | | | | | | | | | | | X | |
| *Leprocaulon albicans* (Th. Fr.) Nyl. ex Hue | | | | | | | | | | | | | | X | |
| *Letrouitia domingensis* (Pers.) Haf. & Bellem. | X | X | | | | | | | | | | | | | |
| *Lopezaria versicolor* (Fée) Kalb & Haffeln. | | X | • | • | X | X | X | X | • | X | • | • | X | | |
| *Megalospora admixta* (Nyl.) Sipm. | | | | | | X | X | X | • | • | X | X | • | • | X |
| *Megalospora tuberculosa* (Fée) Sipm. | | X | • | • | • | • | • | X | • | X | X | X | | | |
| *Melanotheca* sp. A (# 416) | X | | | | | | | | | | | | | | |
| *Ochrolechia pallescens* (L.) Massal. | | | | | X | • | X | X | • | X | | | | | |
| *Pertusaria* spp. | | X | X | X | X | • | X | • | • | X | • | X | X | X | |
| *Phlyctella* spp. | | X | X | X | X | X | | | | | | | | | |
| *Phyllopsora* sp. A (# 427) | X | • | X | • | • | • | X | | | | | | | | |
| *Phyllopsora* spp. | | | X | X | X | • | X | X | X | • | X | • | • | X | |
| *Porina* sp. A (# 330) | X | | | | | | | | | | | | | | |
| *Trypethelium eluteriae* Spreng. | X | | | | | | | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| Macrolichens | | | | | | | | | | | | | | | |
| *Anzia leucobates* (Nyl.) Müll. Arg. | | | | | | | | X | X | X | X | X | X | | |
| *Bulbothrix suffixa* (Stirt.) Hale | | | X | | | | | | | | | | | | |
| *Bulbothrix ventricosa* (Hale & Kurok.) Hale | | | X | X | | | | | | | | | | | |
| *Candelaria concolor* (Dicks.) Stein | X | X | | | | | | | | | | | | | |
| *Candelariella* sp. A (# 290) | | | | X | | | | | | | | | | | |
| *Canomaculina muelleri* (Vain.) Elix & Hale | | | X | | | | | | | | | | | | |
| *Canoparmelia carneopruinata* (Zahlbr.) Elix & Hale | | X | X | • | X | | | | | | | | | | |
| *Canoparmelia caroliniana* (Nyl.) Elix & Hale | | | X | X | X | | | | | | | | | | |
| *Catillaria* sp. A (# 984) | | | | | | | | | | | | | X | | |
| *Cetrariastrum dubitans* Sipm. | | | | | | | | | | | | | X | • | X |
| *Cetrariastrum equadoriense* (Sant.) Sipm. | | | | | | | | | | | | | | | X |
| *Cladonia* cf. *ochrochlora* Flk. | | | | | | | | | X | • | X | X | X | X | X |
| *Cladonia squamosa* (Scop.) Hoffm. var. *squamosa* | | | | | | | | | | | | | X | | |
| *Cladonia subsquamosa* Kremp. | | | | | | | | | | | | | | | X |
| *Coccocarpia domingensis* Vain. | | | | | | | | X | X | | | | | | |
| *Coccocarpia erythroxyli* (Spreng.) Swinscow & Krog | | | | | | X | • | • | • | X | • | X | | | |
| *Coccocarpia pellita* (Ach.) Müll. Arg. em. Sant. | | X | X | X | X | • | X | X | X | | | | | | |
| *Coenogonium* sp. | | | | | | | | | | X | | | | | |
| *Dictyonema glabratum* (Spreng.) D. Hawksw. | | | | | X | X | • | X | X | • | X | X | X | X | X |
| *Dirinaria applanata* (Fée) Awas. | X | X | X | | | | | | | | | | | | |
| *Erioderma sorediatum* Galloway & Jörgensen | | | | | | | | X | | | | | | | |
| *Erioderma* sp. A (# 1281) | | | | | | | | | | X | | | | | |
| *Erioderma verruculosum* Vain. | | | | | | | | X | • | X | • | X | | | |
| *Everniastrum catawbiense* (Degel.) Hale | | | | | | | X | X | X | • | X | X | X | X | |
| *Everniastrum cirrhatum* (Fr.) Hale | | | | | | | | | | | X | X | X | | |
| *Everniastrum fragile* Sipm. | | | | | | | | | | | X | • | • | X | |
| *Heterodermia albicans* (Pers.) Swinscow & Krog | X | • | X | | | | | | | | | | | | |
| *Heterodermia barbifera* (Nyl.) W. A. Weber | | | | | X | X | X | X | | | | | | | |
| *Heterodermia casarettiana* (Massal.) Trevis. | X | X | X | X | X | X | X | X | | | | | | | |
| *Heterodermia* cf. *galactophylla* (Tuck.) W. L. Culb. | | | | | | X | | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Heterodermia circinalis* (Zahlbr.) W. A. Weber | | | | | | | | | | X | | | | | |
| *Heterodermia comosa* (Eschw.) Follm. & Redon | | | | | X | X | X | X | • | X | | | | | |
| *Heterodermia diademata* (Taylor) Awas. | | | | | X | X | X | | | | | | | | |
| *Heterodermia flabellata* (Fée) Awas. | | | | X | • | X | | | | | | | | | |
| *Heterodermia isidiophora* (Nyl.) Awas. | | | | | X | X | | | | | | | | | |
| *Heterodermia leucomela* (L.) Poelt | | X | • | X | X | X | X | X | • | • | X | | | | |
| *Heterodermia lutescens* (Kurok.) Follm. & Redon | | | X | X | X | X | X | X | X | X | | | | | |
| *Heterodermia magellanica* (Zahlbr.) Swinscow & Krog | | | | | | | | X | | | | | | | |
| *Heterodermia microphylla* (Kurok.) Swinscow & Krog | | | | | | | | | | X | • | X | • | • | X |
| *Heterodermia obscurata* (Wulf.) Trevis. | X | X | X | X | X | • | X | X | | | | | | | |
| *Heterodermia speciosa* (Wulf.) Trevis. | X | X | X | X | X | • | X | X | | | | | | | |
| *Heterodermia vulgaris* (Vain.) Follm. & Redon | | | | | X | X | X | X | • | X | X | X | | | |
| *Hypotrachyna andensis* Hale | | | | | | | | | X | X | | | | | |
| *Hypotrachyna bahiana* (Nyl.) Hale | | | | | | | | X | | | | | | | |
| *Hypotrachyna bogotensis* (Vain.) Hale | | | | | | | | | X | X | X | X | X | X | |
| *Hypotrachyna boquetensis* (Hale) Hale | | | | | | | | | | | | | | | X |
| *Hypotrachyna caraccensis* (Taylor) Hale | | | | | | | | | | | | X | X | X | |
| *Hypotrachyna* cf. *pulvinata* (Fée) Hale | | | | | | | | X | | | | | | | |
| *Hypotrachyna costaricensis* (Nyl.) Hale | X | X | X | X | X | • | X | X | X | | | | | | |
| *Hypotrachyna croceopustulata* (Kurok.) Hale | | | X | | | | | | | | | | | | |
| *Hypotrachyna degelii* (Hale) Hale | | | | | X | | | | | | | | | | |
| *Hypotrachyna densirhizinata* (Kurok.) Hale | | | | | | | | X | • | • | • | X | X | X | |
| *Hypotrachyna endochlora* (Leight.) Hale | | | | | X | • | X | X | X | X | | | | | |
| *Hypotrachyna gigas* (Kurok.) Hale | | | | | | | | | | | | X | X | X | |
| *Hypotrachyna imbricatula* (Zahlbr.) Hale | X | X | X | X | X | X | X | X | X | X | X | X | • | X | |
| *Hypotrachyna immaculata* (Kurok.) Hale | | | | | X | | | | | | | | | | |
| *Hypotrachyna isidiocera* (Nyl.) Hale | | | | X | X | • | X | | | | | | | | |
| *Hypotrachyna laevigata* (Smith) Hale group (excl. *H. rockii*) | | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| *Hypotrachyna microblasta* (Vain.) Hale | | | | | X | • | X | X | • | • | X | X | X | X | |
| *Hypotrachyna physcioides* (Nyl.) Hale | | | | | | | | X | • | X | X | X | X | X | X |
| *Hypotrachyna prolongata* (Kurok.) Hale | | | | | | | | | X | • | X | • | X | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Hypotrachyna reducens* (Nyl.) Hale | | | | | X | • | • | X | • | X | X | X | • | X | |
| *Hypotrachyna rhabdiformis* (Kurok.) Hale | | | | | X | • | • | X | • | • | X | | | | |
| *Hypotrachyna rockii* (Zahlbr.) Hale | | | | X | X | | | | | | | | | | |
| *Hypotrachyna sinuosa* (Smith) Hale | | | | | | | | | | | X | X | X | X | X |
| indet folious lichen sp. | | | X | | | | | | | | | | | | |
| *Leciophysma* ? sp. A (# 621) | | | | | | | | | | X | | | | | |
| *Leptogium aciculare* Jörg. | | | | | X | | | | | | | | | | |
| *Leptogium burgesii* (L.) Mont. | | | | | | X | • | X | • | • | X | X | • | X | X |
| *Leptogium coralloideum* (Mey. & Flot.) Vain. | X | X | X | | | | | | | | | | | | |
| *Leptogium foveolatum* Nyl. | | | | | | X | X | | | | | | | | |
| *Leptogium mandonii* Jörg. | | | | | | | | | | | | | | | X |
| *Leptogium marginellum* (Sw.) S. F. Gray | X | X | X | | | | | | | | | | | | |
| *Leptogium phyllocarpum* (Pers.) Mont. | | | | | | | | | | X | | | | | |
| *Leptogium resupinans* Nyl. | | | | | | | | | | X | X | • | • | X | |
| *Leptogium* spp. | X | X | X | X | X | X | X | X | X | X | X | • | • | X | |
| *Lobaria crenulata* (Hook.) Trevis. | | | | | | X | • | X | X | • | X | • | • | X | |
| *Lobaria* spp. | X | X | X | X | X | • | • | X | • | • | X | | | | |
| *Lobaria subexornata* Yoshim. | X | | | | | | | | | | | | | | |
| *Menegazzia* sp. A (# 963) | | | | | | | | | | | X | • | • | X | |
| *Myelochroa lindmannii* (Lynge) Elix & Hale | | | | | X | | | | | | | | | | |
| *Myriotrema concretum* (Fée) Hale | | | | | | | | | | | X | | | | |
| *Nephromopsis* ? sp. A (# 1172) | | | | | | | | | | | | | | | X |
| *Normandina pulchella* (Borr.) Nyl. | | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| *Oropogon bicolor* Essl. | | | | | | | | | X | X | X | X | X | X | X |
| *Oropogon loxensis* (Fée) Th. Fr. | | | | | | | X | X | X | • | X | X | X | X | X |
| *Pannaria conoplea* (Ach.) Bory | | | | | | | | | | | X | | | | |
| *Pannaria mariana* (E. Fr.) Müll. Arg. | | X | X | X | X | | | | | | | | | | |
| *Pannaria rubiginosa* (Ach.) Bory | | | | | X | X | • | X | • | X | • | • | • | X | X |
| *Pannaria* sp. A (# 1231) | | X | | | | | | | | | | | | | |
| Pannariaceae | | | | | | | | | | | | | | | X |
| *Parmeliella nigrocincta* (Mont.) Müll. Arg. | | | | | | | | | | | | | | | X |
| *Parmeliella* sp. A (# 1081) | | | | X | X | | | | | | | | | | |
| *Parmelina* sp. A (# 1185) | | | | | | | | | | | | | | | X |
| *Parmelinopsis spumosa* (Asah.) Elix & Hale | | | X | X | | | | | | | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Parmotrema* cf. *austrosinense* (Zahlbr.) Hale | | | | X | | | | | | | | | | | |
| *Parmotrema guyanum* Hale | | X | X | • | X | • | X | | | | | | | | |
| *Parmotrema haitiense* (Hale) Hale | X | X | X | X | X | | | | | | | | | | |
| *Parmotrema mellissii* (Dodge) Hale | | X | X | X | X | | | | | | | | | | |
| *Parmotrema peralbidum* (Hale) Hale | | | | | X | • | X | X | X | | | | | | |
| *Parmotrema robustum* (Degel.) Hale | | | | | X | | | | | | | | | | |
| *Parmotrema sancti-angeli* (Lynge) Hale | | X | X | X | | | | | | | | | | | |
| *Parmotrema subsumptum* (Nyl.) Hale | | X | X | X | X | X | | | | | | | | | |
| *Parmotrema tinctorum* (Wyl.) Hale | | X | X | X | | | | | | | | | | | |
| *Parmotremopsis antillensis* (Nyl.) Elix & Hale | | | | X | | | | | | | | | | | |
| *Peltigera dolichorhiza* (Nyl.) Nyl. | | | | | | | | X | | | | | | | |
| *Peltigera pulverulenta* (Taylor) Nyl. | | | | | | | | | | | | | | | X |
| *Phaeophyscia hispidula* (Ach.) Moberg | | | X | | | | | | | | | | | | |
| *Physcia atrostriata* Moberg | X | X | | | | | | | | | | | | | |
| *Physcia erumpens* Moberg | X | X | X | X | X | | | | | | | | | | |
| *Physcia integrata* Nyl. | | | | X | X | | | | | | | | | | |
| *Physcia lobulata* Moberg | | | | X | | | | | | | | | | | |
| *Physcia poncinsii* Hue | | | X | X | X | | | | | | | | | | |
| *Physcia sorediosa* Moberg | X | • | X | | | | | | | | | | | | |
| *Physcia verrucosa* Moberg | | | | X | X | X | | | | | | | | | |
| Physciaceae | X | X | • | X | | | | | | | | | | | |
| *Polychidium dendriscum* (Nyl.) Henssen | | | | | | | | X | X | | | | | | |
| *Pseudocyphellaria aurata* (Ach.) Vain. | | | | | X | X | • | X | | | | | | | |
| *Pseudocyphellaria intricata* (Delile) Vain. | | | | | | | | | | | X | | | | |
| *Punctelia rudecta* (Ach.) Krog | | | | X | X | | | | | | | | | | |
| *Pyxine caesiopruinosa* (Tuck. in Nyl.) Imsh. | X | X | • | X | X | | | | | | | | | | |
| *Pyxine coralligera* Malme | | X | | | | | | | | | | | | | |
| *Pyxine eschweileri* (Tuck.) Vain. | | | X | | | | | | | | | | | | |
| *Pyxine subcinerea* Stirt. | | | X | | | | | | | | | | | | |
| *Ramalina celastri* (Spreng.) Swinscow & Krog | | X | X | X | X | • | X | | | | | | | | |
| *Ramalina cochlearis* Zahlbr. | | | | X | X | X | X | X | • | X | | | | | |

TABLE 2. Continued.

| | Altitude (m) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,000 | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | 4,130 |
| *Ramalina* sp. A (# 793) | | | | | | | X | X | X | • | X | X | X | | |
| *Ramalina* sp. sect. *inflata* (# 1236) | | | X | X | | | | | | | | | | | |
| *Rimelia commensurata* (Hale) Hale & Fletcher | | X | X | X | | | | | | | | | | | |
| *Rimelia reticulata* (Taylor) Hale & Fletcher | | X | X | X | X | • | X | X | | | | | | | |
| *Rimelia subisidiosa* (Müll. Arg.) Hale & Fletcher | | X | X | • | X | | | | | | | | | | |
| *Sphaerophorus formosanus* (Zahlbr.) Asah. | | | | | | | X | • | X | • | X | X | X | X | |
| *Sticta* cf. *damaecornis* (Sw.) Ach. | | | | | | | | | | | X | • | X | X | |
| *Sticta* cf. *laciniata* (Sw.) Ach. | | | | | X | • | • | X | • | • | X | X | | | |
| *Sticta fuliginosa* (Dicks.) Ach. | | | | | | X | X | X | • | X | • | • | • | X | |
| *Sticta* spp. | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |
| *Sticta weigelii* (Isert.) Ach. | X | X | X | X | X | • | X | • | X | X | | | | | |
| *Teloschistes flavicans* (Sw.) Norm. | | X | X | X | • | X | • | • | • | X | | | | | |
| *Teloschistes hypoglaucus* (Nyl.) Zahlbr. | | | | X | | | | | | | | | | | |
| *Usnea* spp. | X | X | X | X | X | X | X | X | X | X | X | X | X | X | X |

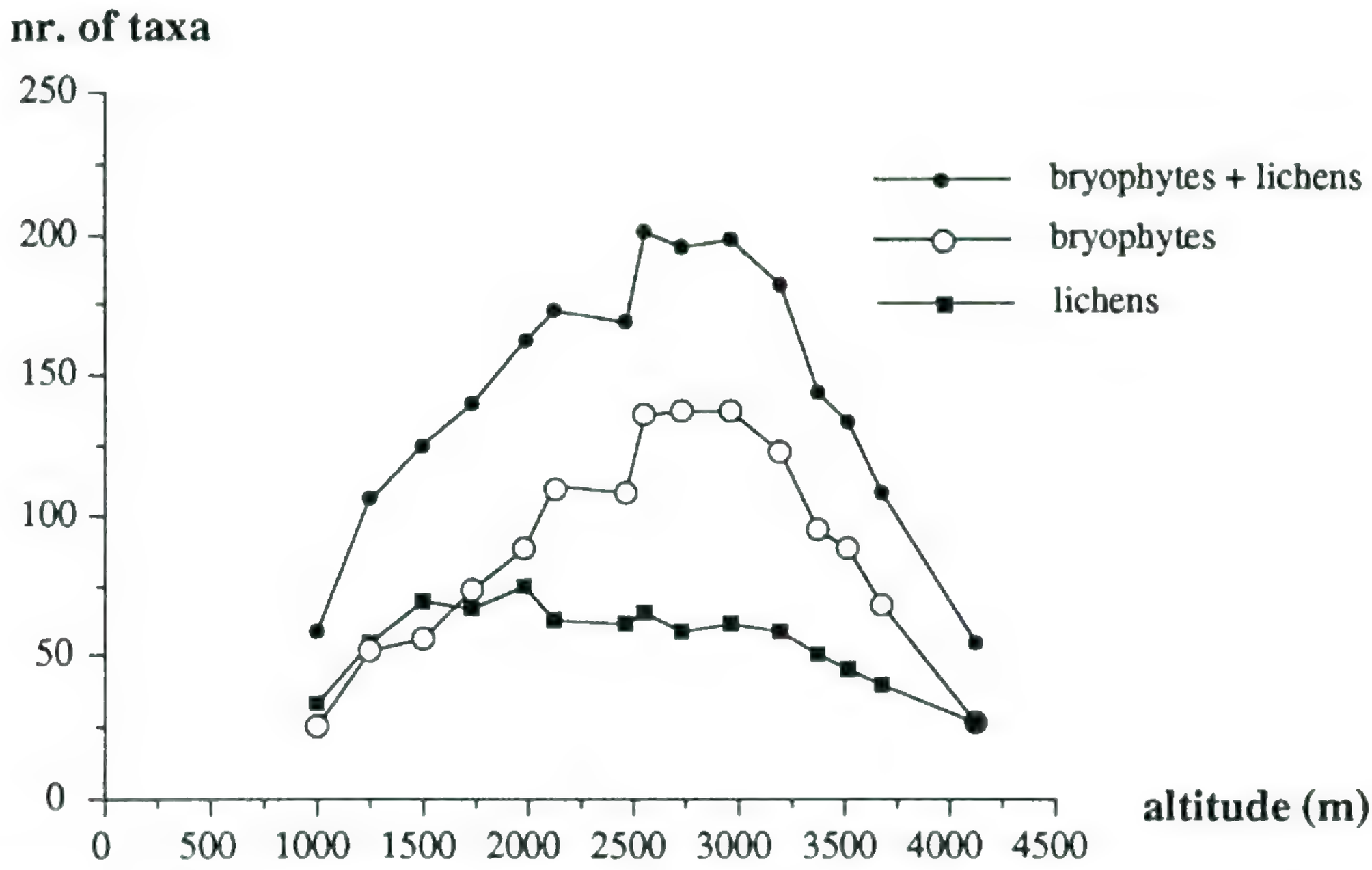



FIGURE 10. Distribution pattern of bryophyte and lichen richness in relation to altitude, as derived from Table 2.

and 3,200 m and substantially at higher altitudes. While foliose and crustose lichen taxa numbers tend to drop with altitude, fruticose lichen numbers increase up to an altitude of about 3,400 m (Fig. 11). The bryophyte curve (Fig. 12) is mainly determined by the liverwort component, whereas mosses exhibit very much the same distribution as the overall lichen pattern.

The mosses : liverworts ratio has been repeatedly correlated to humidity (Gradstein et al., 1989; van Reenen & Gradstein, 1983) and the data on epiphytic bryophytes, including canopy species, for altitudes up to ca. 3,200 m confirm the hypothesis that the contribution of liverworts to overall bryophyte diversity increases with humidity.

Liverworts are an important element, in terms

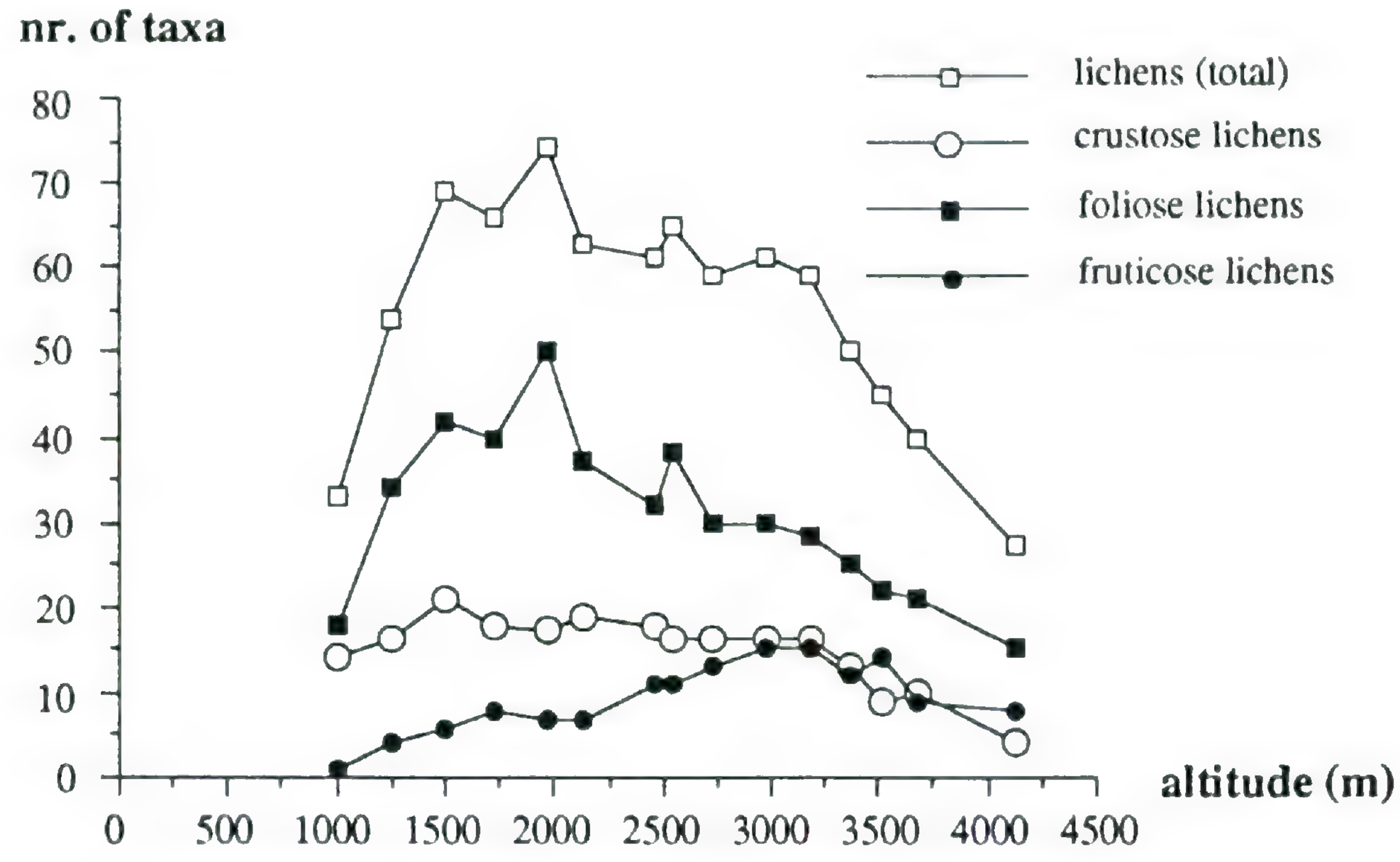



FIGURE 11. Distribution pattern of lichen richness in relation to altitude, as derived from Table 2.

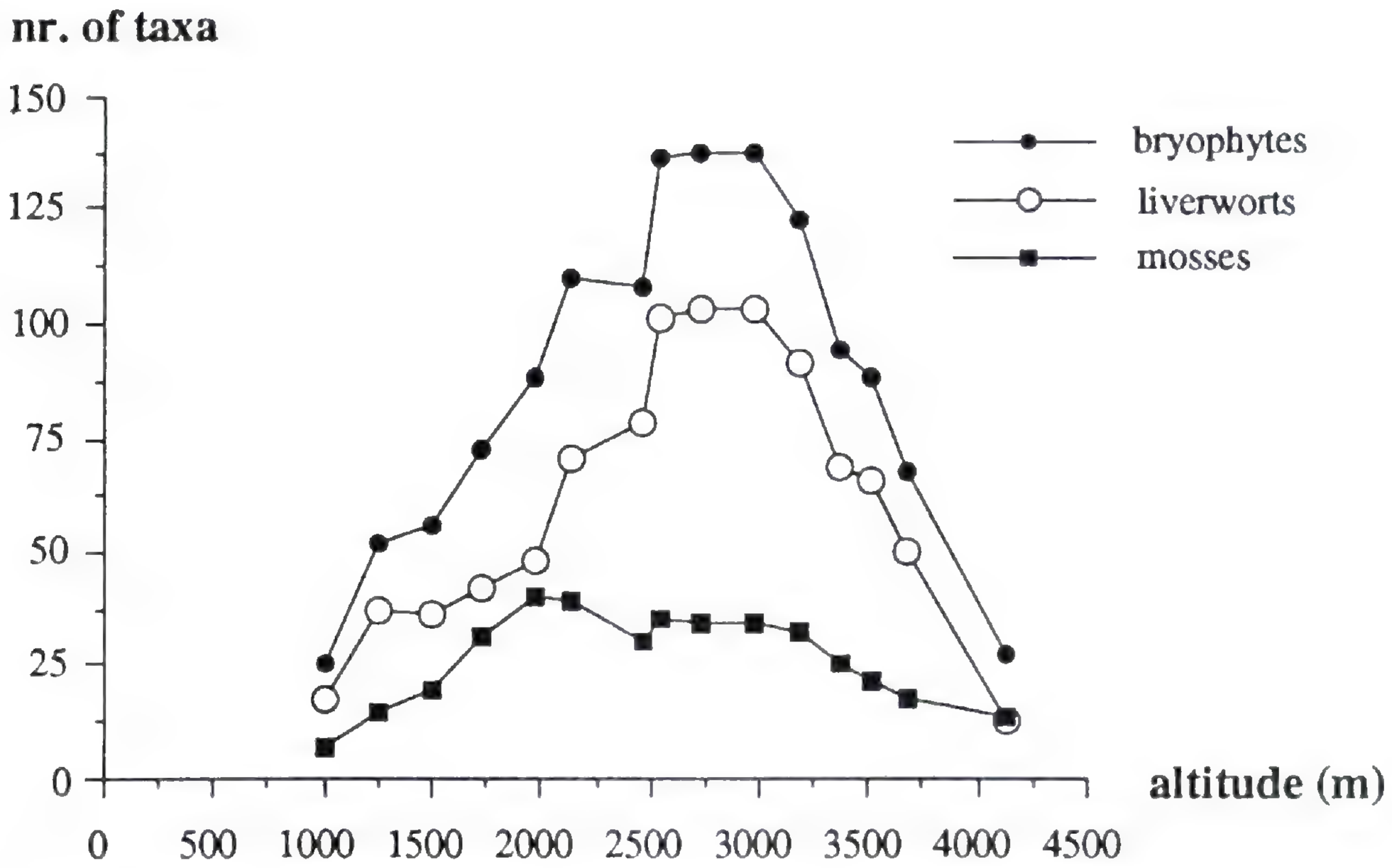



FIGURE 12. Distribution pattern of bryophyte richness in relation to altitude, as derived from Table 2.

of species numbers, of the epiphytic flora, and reach maximum species richness between 2,550 m and 3,190 m (Fig. 12). Shmida & Wilson (1985) proposed two hypotheses, besides niche relations and habitat diversity (e.g., MacArthur, 1965), to explain how species diversity along a macrogradient can be caused and maintained: mass effect and ecological equivalency. Mass effect is the establishment of species in sites where they cannot be self-maintaining, and ecological equivalency is the coexistence of species within the same fundamental niche.

The mass effect hypothesis requires the existence of an adjacent core area from which there is a steady influx of propagules to the site. In practice it is not always easy to establish whether a species will be able to survive at a site.

The mass effect hypothesis is attractive for epi-

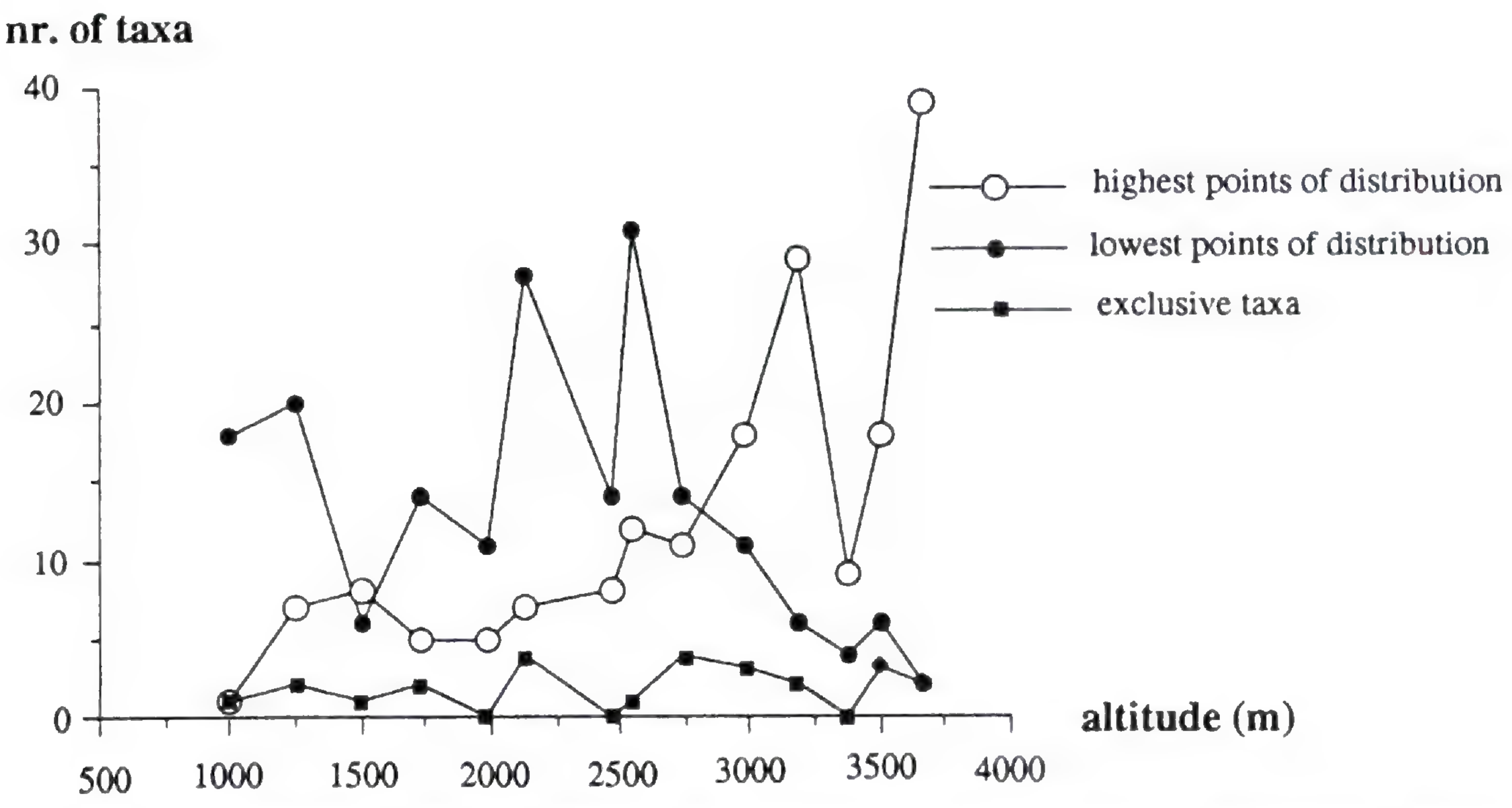



FIGURE 13. Distribution of taxa of liverworts along the altitudinal gradient; number of exclusive taxa for each altitude and number of endpoints of species ranges.

TABLE 3. Average position of sites along the first axis of ordination as generated by Detrended Correspondence Analysis. Scaling of the axis in units of standard deviation (s.d. units) × 100 (Hill, 1979).

| | Site altitude (m) | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1,250 | 1,500 | 1,725 | 1,980 | 2,130 | 2,460 | 2,550 | 2,740 | 2,970 | 3,190 | 3,370 | 3,510 | 3,670 | | | | | | | |
| Eigenvalue axis ½ | | | | | | | | | | | | | | | | | | | | |
| All data | 0.613/0.131 | 386 | 372 | 325 | 283 | 224 | 182 | 133 | 98 | 83 | 58 | 26 | 2 | 0 | | | | | | |
| Macrolichens | 0.630/0.137 | 357 | 360 | 341 | 274 | 204 | 174 | 138 | 101 | 80 | 42 | 18 | 0 | −11 | | | | | | |
| Liverworts | 0.613/0.095 | 430 | 404 | 306 | 283 | 228 | 192 | 131 | 101 | 88 | 70 | 30 | 7 | 0 | | | | | | |
| Mosses | 0.730/0.096 | 528 | 478 | 446 | 396 | 345 | 261 | 217 | 158 | 151 | 107 | 44 | 0 | 0 | | | | | | |
| Bryophytes | 0.646/0.089 | 454 | 422 | 351 | 321 | 264 | 212 | 156 | 118 | 106 | 81 | 34 | 8 | 0 | | | | | | |

phytic bryophytes and lichens. First, many lichens and bryophytes often produce spores in abundance (Richards, 1984) and/or have extensive vegetative reproduction; parts of the plants just break off or special structures are formed, like gemmae in mosses and soralia or isidia in lichens. While data on dispersal efficiency of bryophytes and lichens are difficult to obtain, some impression may be obtained by the high speed of colonization of new available sites.

Second, in a frequently disturbed habitat it will be easier for propagules to find a suitable (vacant) site to establish themselves. The epiphytic habitat is likely to have a high rate of disturbance due to the exfoliation of bark fragments, the occurrence of tree or branch fall, and disturbances by animals such as mammals (Perry, 1978b), birds (nesting material, nesting sites, and invertebrate foraging; Nadkarni & Matelson, 1989), and invertebrates (pathways of leaf cutter ants; pers. obs.).

According to Shmida & Wilson (1985), the influence of ecological equivalency on overall richness should be highest in systems in which habitats are patchily distributed (isolated branches) and/or in which competitive interactions are reduced. As to competition, indications are that bryophyte communities are not at competitive equilibrium (Slack, 1977; Watson, 1980), and that competitive interactions between bryophytes are not very intense (During & ter Horst, 1987; During and van Tooren, 1988).

Mass effect and ecological equivalency hypotheses, in combination with overlapping species ranges, predict the highest species diversity at transition zones, where two distinct floras meet (= contact transition). The distribution patterns of individual liverwort taxa along the elevational gradient (Fig. 13) show that at 2,130 m many taxa have their lowest point of distribution, coinciding with a marked decrease of humidity below this altitude (Figs. 5, 6). A second peak in "points of lowest distribution" at 2,550 m indicates the first occurrence of many liverwort species characteristic of the higher (altitudinal) forest, e.g., *Lepicolea pruinosa* (Tayl.) Spruce, *Jamesoniella rubricaulis* (Nees) Grolle, and several *Herbertus* species. At an altitude of 3,190 m many species from lower altitudes reach their upper limit, e.g., *Taxilejeunea pterigonia* (Lehm. & Lindenb.) Schiffn., *Frullania caulisegua* (Nees) Nees (=*F. obcordata*), and *Plagiochila bursata* (Desv.) Lindenb. The difference in maxima between points of lowest and of highest altitudinal distributions demonstrates the presence of a zone of overlap between 2,550 and 3,190 m. This transition zone coincides nicely with the belt

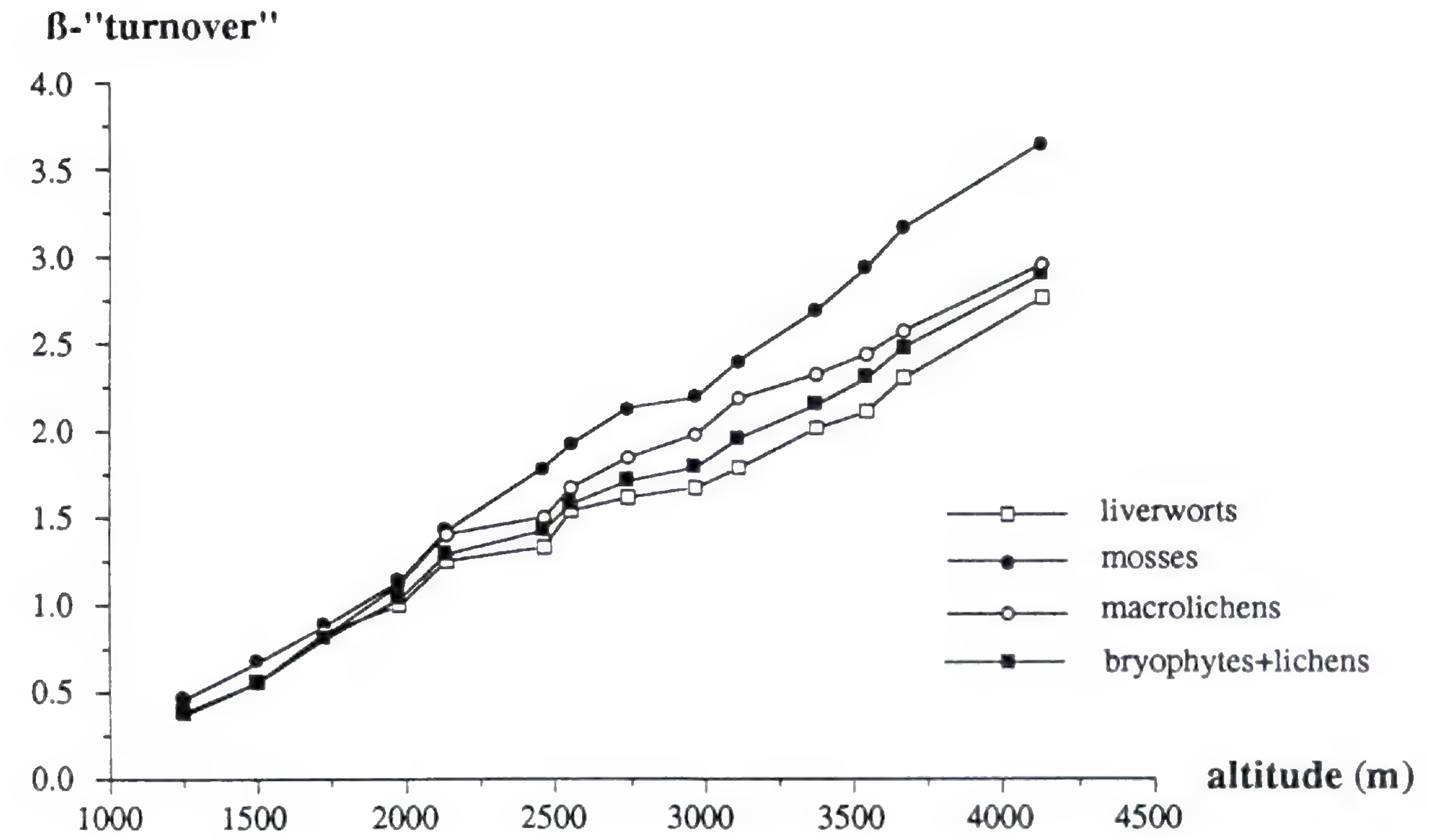



FIGURE 14. Beta diversity along the altitudinal gradient, using the Wilson & Shmida (1984) measure, or "beta turnover," of diversity.

of highest species richness (Fig. 12), as predicted. However, induced floristic transition zones, where a sharp environmental boundary in a gradient is present, have a great variety of species as well, but this type of transition zone is likely to have species centered in it. On the total of 127 taxa of liverworts occurring in the transition zone, there are 101 taxa (ca. 80%) that occur outside this altitudinal range as well and each altitude sampled within this range has only 2–6 (= <10%) exclusive species (Fig. 13). The bryophyte floras from lower and higher elevations in the transect are from a different origin, as demonstrated by Gradstein et al. (1989). They concluded: "It appears that at lower altitudes, below 3,000 m, wide ranging tropical species prevail whereas narrow ranging tropical species and species of temperate origin are more common at higher altitudes."

## BETA DIVERSITY PATTERNS

Relative site position along the first axis of ordination, using DECORANA (Table 3), may be seen as a reliable estimate of species turnover, when the gradient is unidimensional (Økland, 1986), as shown by the much higher eigenvalues of the first axis than of the second axis. For macrolichens, mosses, and liverworts, Spearman's rank coefficients for correlation between ordination rankings of sites along the first axis and altitude are highly significant ($R \geq 0.989$; $P < 0.001$). Altitude, a complex ecological factor, thus explains well the variation in the data for these taxonomic groups.

Macrolichens generally have a greater altitudinal range than liverworts and mosses, indicated by a shorter first axis of ordination of, respectively, 3.68 s.d., 4.30 s.d., and 5.28 s.d. Lichens were shown to have wider amplitudes than bryophytes (mainly mosses) in relation to latitudinal and edaphic (pH, texture, and moisture) gradients in the Canadian subarctic forest tundra as well (Robinson et al., 1989) and along a potential evapotranspiration gradient and a gradient based on Conrad's index of continentality in pine forests in Finland (Oksanen, 1983).

Mosses apparently are more specialistic than liverworts (Table 3), a conclusion also reached by Florschütz-de Waard & Bekker (1987) studying different types of lowland forest in Suriname.

The change in beta diversity on the altitudinal gradient, using Wilson & Shmida's (1984) measure, "beta turnover," reveals that the overall more specialistic behavior of mosses may in particular be attributed to the greater species turnover of mosses at altitudes above 2,130 m (Fig. 14).

Lee & La Roi (1979) compared half change values (Whittaker, 1960) of bryophytes along an altitudinal gradient in Canada with values derived from studies by Slack (1977) in the United States. Half change values along altitudinal coenoclines

TABLE 4. Half changes of elevational coenoclines in temperate and tropical America. (1) From Slack (1977), coenocline: length 970 m, mid-elevation ca. 1,000 m; (2) from Lee & La Roi (1979), coenocline: length 1,250 m, mid-elevation ca. 1,100 m; (3) this study, coenocline: length 1,000 m, mid-elevation 1,750 m (a) and 3,170 m (b).

| | | Bryophytes | Macrolichens | Bryophytes/ macrolichens |
|---|---|---|---|---|
| Adirondack Mountains, New York, U.S.A. | (1) | ca. 1.26 | — | — |
| Jasper National Park, Canada | (2) | 1.1 | — | — |
| Colombia (a) reference stand: 1,250 m | (3) | 1.45 | 0.93 | 1.26 |
| (b) reference stand: 3,670 m | (3) | 1.30 | 0.94 | 1.22 |

are presented in Table 4. Semi log regressions used for the calculation of half changes in Colombia all had $R^2$ values of over 0.92. Contrary to indications given by beta turnover values (Fig. 14), bryophytes and macrolichens do appear to have a different rate of biotic change at lower altitudes, with half changes of 1.45 and 0.93, respectively. A possible explanation may be methodological. Half change values are calculated using similarity values of sites to a reference (first) stand. While for the other sites in the coenocline some correction is possible for outliers by means of the regression used, the composition of the first stand is determinant. Beta turnover as measure does not attach extra weight to one of the stands.

Half change values in the tropical mountains of Colombia are greater, especially for the "1,250 m coenocline," than have been reported for temperate North American mountains, indicating narrower species ranges in the tropics in relation to altitude as predicted by Janzen (1967) and documented for lizards, frogs, and snakes (Huey, 1978). However, present data on bryophytes should be regarded with caution, since the number of substrate types between studies varied. Whereas this study was limited to epiphytes, Slack's (1977) study included bryophytes from a wide range of both epiphytic and terrestrial substrate types, and Lee & La Roi (1979) sampled the three most abundant terrestrial substrates only in each stand. Including bryophytes from more substrate types in the analysis will lead to a higher species turnover, as remarked by Lee & La Roi (1979), not invalidating the general conclusion. Furthermore, actual species turnover in the present study is higher than recorded because of occasional species lumping.

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# CHROMOSOME CYTOLOGY OF THE AFRICAN GENUS *LAPEIROUSIA* (IRIDACEAE–IXIOIDEAE)[1]

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ABSTRACT

Chromosome counts, now available for 33 of the approximately 40 species of *Lapeirousia*, show the genus to be remarkably variable cytologically. Excluding polyploidy, numbers range from $n = 10$ to 9, 8, 7, 6, 5, 4, and 3 in what we believe to be a descending dysploid series. A cycle of polyploidy and secondary descending dysploidy appears to have occurred in the tropical African section *Paniculata*. In *L. erythrantha* of the section there are both diploid populations with $n = 4$ and polyploid populations with $n = 6$, the latter karyotype having about twice as much chromosome material as the $n = 4$ karyotype. Although chromosome numbers vary among the species, the single large chromosome pair and total amount of chromosome material appear to be conserved, indicating the progressive fusion of small chromosomes, from a putatively ancestral bimodal karyotype with one long and nine short chromosome pairs. A phylogeny for section *Paniculata* is proposed based largely on karyotype change. An unusually high frequency of B chromosomes is evident in species with higher chromosome numbers. Not before detected, their irregular presence in populations probably explains past difficulty in determining chromosome numbers in several species of the genus.

Chromosome cytology is an important factor in considerations of the systematics and phylogeny of *Lapeirousia*, a widespread African genus of Iridaceae subfamily Ixioideae. The estimated 40 species of the genus (Goldblatt & Manning, in prep.) are currently divided among two subgenera, subgenus *Lapeirousia* with sections *Lapeirousia* and *Sophronia*, and subgenus *Paniculata* with sections *Paniculata* and *Fastigiata* (Goldblatt & Manning, 1990; Goldblatt, 1990a; Goldblatt & Manning, 1992). That the chromosome cytology of *Lapeirousia* is extremely variable is well known (Goldblatt, 1990b): excluding polyploidy, base numbers range from $x = 10$ to 3. Such variability is remarkable in plants in general, including Iridaceae, most genera of which exhibit little or no variation in basic number (Goldblatt, 1971).

Based on outgroup comparison, ancestral base number in *Lapeirousia* is most likely $x = 10$, but species of *Lapeirousia* with $2n = 20$, 18, 16, and some with $2n = 12$ or 10 are distinctive in having strongly bimodal karyotypes with one long chromosome pair and nine to four smaller pairs less than half as long as the long pair. Only in the predominantly tropical African section *Paniculata* are there departures from this pattern, and most species have karyotypes with chromosomal rearrangements that have resulted in derived base numbers of $x = 6$, 5, 4, and 3. Among these is the widespread and diverse *L. erythrantha*, which until now has been thought to be a hypotetraploid with a secondary base of $n = 6$, derived from ancestors with $n = 4$ (Goldblatt, 1990b). New counts presented here for *L. erythrantha* confirm $2n = 12$ in some Zimbabwean populations, but we have found other populations both in Zimbabwe and Zaire with $2n = 8$. These and several more new counts of both tropical and southern African species shed new light on the cytology of *Lapeirousia* and show an unexpected frequency of B chromosomes in several species. We believe that B chromosomes are responsible for some of the apparent intraspecific chromosomal variability in base number reported in several species of the genus and uncertainty about the correct number in others (Goldblatt, 1972, 1990b). Consequently, we also review cytological patterns throughout the genus.

## MATERIAL AND METHODS

Seeds or corms of wild-collected species (Appendix) were sprouted in the greenhouse, and emer-

[1] Support for this study by grants BSR 8500148 and 8906300 from the U. S. National Science Foundation is gratefully acknowledged. We thank Jane Masterson and Hewson Swift, University of Chicago, for cytophotometric estimations of total DNA per genome in selected species.

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gent leaf and root tips were harvested for analysis of mitosis in one of two ways. For rapid determination of chromosome number, root tips were pretreated in saturated aqueous m-bromonapthalene for 4 hours at room temperature, then fixed in 3:1 absolute ethanol-glacial acetic acid for 5 minutes. After hydrolysis in 10% HCl at 60°C for 6 minutes, tips were squashed in FLP orcein (Jackson, 1973). For more critical analysis, leaf and root tips were pretreated in 0.002 M aqueous 8-hydroxyquinoline for 4–5 hours at room temperature, then fixed in modified Carnoy's solution (absolute ethanol-glacial acetic acid-chloroform 6 : 3 : 1) at 8°C for about 24 hours. Both root and leaf tips were stained in Feulgen reagent and squashed in 1% aceto-orcein. Photographed preparations were all made using the latter technique. For purposes of comparison we included one species of *Watsonia*, which belongs to the same tribe Watsonieae as *Lapeirousia*, and *Pillansia templemanni*, only genus of Pillansieae, and outgroup to Watsonieae, in the study.

Comparative genome size (Table 1) was estimated by calculating total chromosome length in metaphase karyotypes of comparably condensed chromosomes, always treated in exactly the same manner. Since chromosomes are not always contracted to exactly the same degree, this method is not completely reliable. It is, however, sufficient to distinguish different ploidy levels. Accurate cytophotometric determinations made by Jane Masterson using *Nicotiana tabaccum* as a standard (Table 2) confirm our hypothesis that the $2n = 12$ cytotype of *Lapeirousia erythrantha* is polyploid, as are the karyotypes of *L. otaviensis* and *L. schimperi*.

## Observations

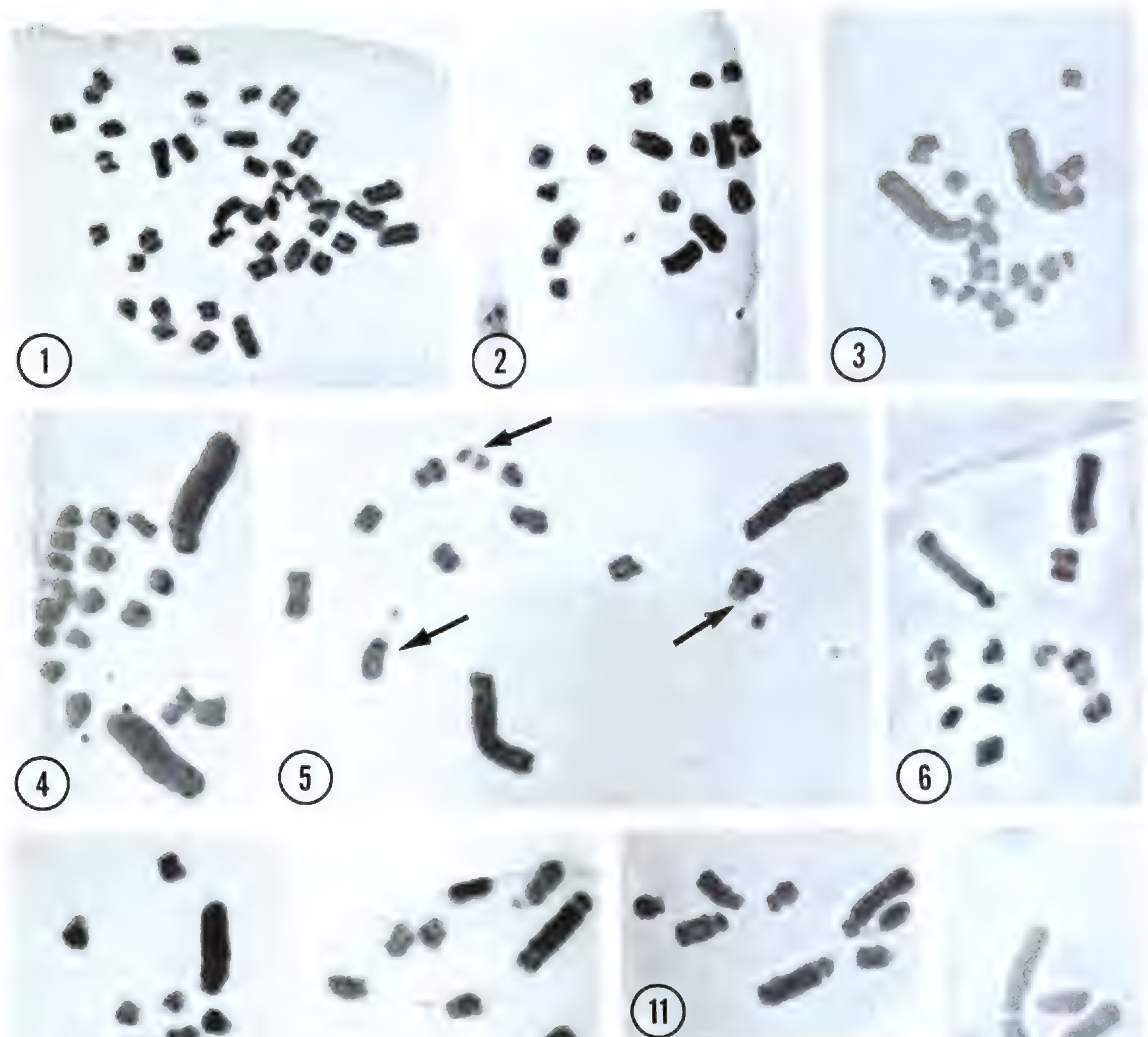
*Number and size.* Chromosomes of *Pillansia*, *Watsonia*, and *Lapeirousia* are moderate to small in size (Figs. 1–25), with either modest, or, in most species of *Lapeirousia*, with considerable range in number and size (Table 1). Total length variation across *Lapeirousia*, excluding B chromosomes, is 0.9–7.6 μm. In *Pillansia* and *Watsonia coccinea* chromosomes are comparable in size (Figs. 1, 2, 27A, B), but all fairly small, 0.7–4 μm long.

Chromosome number is consistently $2n = 20$ in *Lapeirousia* sect. *Fastigiata* (Table 1; Figs. 3, 4), but in the other section of subgenus *Paniculata*, sect. *Paniculata*, numerical range is extreme, with the highest number $2n = 16$ and the lowest $2n = 6$ (Table 1). In subgenus *Lapeirousia* diploid numbers of $2n = 18$ and 16 occur in section *Sophronia* (Table 1; Figs. 16–23) while all species of section *Lapeirousia* so far counted have $2n = 16$ (Figs. 19, 24, 25). With decrease in number there is an apparent gradual increase in size of one or more chromosome pairs (Table 1).

*Karyotypes.* Bimodal karyotypes characterize *Watsonia* and the majority of species of *Lapeirousia*, including all those of subgenus *Lapeirousia* and subgenus *Paniculata* sect. *Fastigiata*. Although four longer chromosome pairs also stand out in *Pillansia* (Fig. 1, 27A), size differences are too gradual for the karyotype to be characterized as strictly bimodal. In *Watsonia* (Figs. 2, 27B) there are two long chromosome pairs but always just one long pair in bimodal karyotypes in *Lapeirousia*. In *Lapeirousia* these long chromosomes are 4.1–6.5 μm long, and the remainder are generally 1–2 μm long, arbitrarily characterized here as small or medium (Table 1). We are uncertain of the reason for the variation in the length of the long pair among the species, although we believe that this pair is homologous across the genus because of its distinctive prophase morphology (see below). Differential contraction at metaphase due to preparation or enlargement of the chromosomes across the entire karyotype could explain the differences we have observed.

In species with bimodal karyotypes and $2n = 20$ (section *Fastigiata*) all 18 of the smaller chromosomes are small (less than 2 μm long according to our arbitrary criterion for categorizing the chromosomes by size). Bimodal karyotypes with $2n = 18$ (some species of section *Sophronia*) have two of the smaller chromosomes appreciably larger than the remainder, and these fall into our medium category. In bimodal karyotypes with $2n = 16$ (some species of section *Sophronia* and all species of section *Lapeirousia* examined) two pairs fall in our medium group.

In section *Paniculata* the typical bimodal karyotype with one long pair and many smaller ones occurs in *Lapeirousia avasmontana* ($2n = 16$), *L. gracilis* and *L. neglecta* (both $2n = 12$) and *L. sandersonii* ($2n = 10$) (Figs. 6, 7, 9). In *L. gracilis* two of the small chromosome pairs fall in our medium category. Bimodality is less pronounced in *L. setifolia*, *L. abyssinica*, and the $2n = 8$ karyotype of *L. erythrantha* (Figs. 10, 11). The karyotypes of *L. rivularis* and the $2n = 12$ cytotype of *L. erythrantha* show no bimodality (Figs. 12, 13). In *L. schimperi* and *L. otaviensis*, $2n = 10$, there is a secondary development of bimodality with a long metacentric pair 6.9–7.6 μm long, about one-third again as long as the next longest pair (Figs. 14, 15). In *L. schimperi* this




FIGURES 1–13. Mitotic metaphase in *Pillansia*, *Watsonia*, and *Lapeirousia* subgenus *Paniculata*.—1. *P. templemanii*.—2. *W. coccinea*.—3. *L. corymbosa*.—4. *L. azurea*.—5. *L. gracilis*, cytotype with 3 satellite chromosomes.—6. *L. gracilis*, cytotype with one satellite chromosome.—7. *L. neglecta*.—8. *L. coerulea*.—9. *L. sandersonii*.—10. *L. setifolia*.—11. *L. erythrantha*, $2n = 8$ cytotype.—12. *L. erythrantha*, $2n = 12$ cytotype.—13. *L. rivularis*. Vouchers as given in Table 1. Scale bar, 5 μm.

FIGURES 14–25. Mitotic metaphase in *Lapeirousia* subg. *Paniculata* (14 and 15) and subgenus *Lapeirousia* (16–25).—14. *L. otaveinsis*.—15. *L. schimperi*.—16. *L. pyramidalis*.—17. *L. silenoides*.—18. *L. exilis*.—19. *L. jacquinii*.—20. *L. littoralis* subsp. *caudata*.—21. *L. odoratissima*.—22. *L. oreogena*, cytotype with 2 large B chromosomes.—23. *L. oreogena*, cytotype without B chromosomes.—24. *L. arenicola*.—25. *L. dolomitica* subsp. *lewisiana*. Vouchers as given in Table 1. Scale bar, 5 μm.

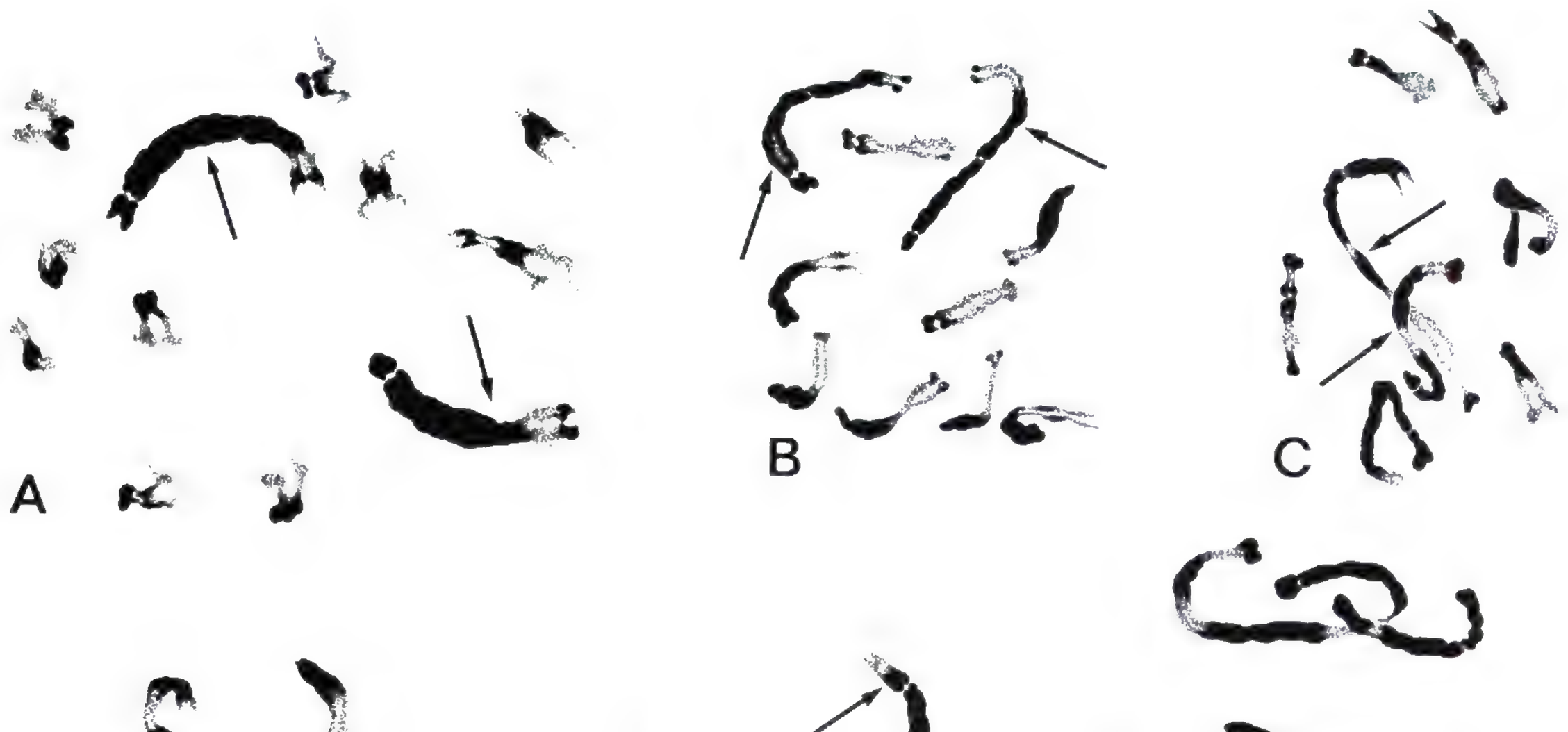



FIGURE 26. Mitotic prophase in selected species of *Lapeirousia*.—A. *L. neglecta*.—B. *L. sandersonii*.—C. *L. coerulea*.—D. *L. erythrantha*, $2n = 8$ cytotype.—E. *L. erythrantha*, $2n = 12$ cytotype.—F. *L. schimperi*. Scale bar, 5 μm. Arrows indicate the long chromosome pair with characteristic appearance.

second pair has a prophase staining pattern that suggests homology with the long chromosome pair in the karyotypes of other species (Fig. 26). *Lapeirousia otaviensis* has two karyotypes among the plants we examined. In one, presumably the ancestral type, the chromosomes closely resemble those of *L. schimperi*, except that the second longest pair is metacentric, whereas in *L. schimperi* the shortest pair is submetacentric and second longest pair is acrocentric. Generally, only one satellite is visible, located on one of the two fourth longest chromosomes. The other karyotype in *L. otaviensis* is heterozygous for a translocation involving one of the second longest pair and one other chromosome. There is thus only one member of the second longest pair and only one very short, nearly telocentric chromosome. This karyotype also normally has only one satellite chromosome. Despite these irregularities, the similarity to the karyotype of *L. schimperi* is striking.

*Satellite position.* A pair of small satellites, located on the short arms of the longest pair of small chromosomes, are frequently present in species of *Lapeirousia* with bimodal karyotypes (Figs. 3–10, 16–21). Two pairs of satellites are present in *L. coerulea* ($2n = 8$) and the $2n = 8$ karyotype of *L. erythrantha* (Figs. 8, 11). In *L. dolomitica* subsp. *lewisiana* ($2n = 16$) one of the two pairs of satellites are very large (about as long as the long chromosome arms) and the short arms are minute; the second pair of satellites are also unusually large and slightly exceed the short chromosome arms in length (Fig. 25). In *L. azurea* ($2n = 20$), *L. silenoides* ($2n = 18$), *L. littoralis*, and *L. oreogena* (both $2n = 16$), all of which also have two pairs of satellites, both satellite chromosome pairs have short arms shorter than the satellites. The situation in *L. gracilis* is puzzling: two cytotypes (Figs. 5, 6) differing in satellite number and morphology are present in the same pop-

TABLE 1. Chromosome numbers, total chromosome length (diploid), and karyotype features in *Lapeirousia*. Counts obtained here (Appendix 1) are combined with those previously published (Goldblatt, 1971, 1972, 1990a). Species are arranged within sections according to karyotypic similarity. Abbreviations: L = Large (>4 μm), M = medium (2–4 μm), S = small (<2 μm), m = metacentric, sm = submetacentric, a = acrocentric, – = data not available. Total chromosome length was determined by linear measurement of photographed karyotypes, prepared in exactly the same manner. Data are not directly comparable with the measurements of Goldblatt (1990b) for the same species due to the different method of preparation. B chromosomes are not included in the measurements of total chromosome length or descriptive statistics.

| Species | Diploid number | Total chromosome length μm | Karyotype features | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Size | | | Morphology | | |
| | | | L | M | S | m | sm | a |
| *Lapeirousia* | | | | | | | | |
| Subgenus *Paniculata* | | | | | | | | |
| Section *Fastigiata* | | | | | | | | |
| *L. corymbosa* (L.) Ker Gawl. | 20 | 31.5 | 2 | 0 | 18 | ←18→ | | 2 |
| *L. azurea* (Eckl. ex Baker) Goldblatt | 20 | 38.4 | 2 | 0 | 18 | ←18→ | | 2 |
| *L. falcata* (L.f.) Ker Gawl. | 20 | – | 2 | 0 | 18 | ←18→ | | 2 |
| *L. micrantha* (E. Meyer ex Klatt) Baker | 20 | – | 2 | 0 | 18 | ←18→ | | 2 |
| Section *Paniculata* | | | | | | | | |
| *L. avasmontana* Dinter | 16 | – | 2 | 0 | 14 | ←14→ | | 2 |
| *L. gracilis* Vaupel | 12 | 26.2 | 2 | 4 | 6 | ←10→ | | 2 |
| *L. neglecta* Goldblatt | 12 | 26.2 | 2 | 0 | 10 | ←10→ | | 2 |
| *L. sandersonii* Baker | 10 | 28.6 | 2 | 4 | 4 | ←8→ | | 2 |
| *L. abyssinica* (A. Rich.) Baker | 8 | – | 4 | 2 | 2 | 2 | 2 | 4 |
| *L. coerulea* Schinz | 8 | 27.6 | 4 | 4 | 0 | ←6→ | | 2 |
| *L. setifolia* Harms | 8 | 25.4 | 2 | 4 | 2 | 0 | 2 | 6 |
| *L. erythrantha* (Klotzsch ex Klatt) Baker | 8 | 24.5 | 2 | 4 | 2 | 0 | 4 | 4 |
| | 12 (+ 0 – 3B) | 54.1 | 8 | 4 | 0 | 0 | 0 | 12 |
| *L. rivularis* Wanntorp | 12 | 47.2 | 6 | 6 | 0 | 0 | 2 | 10 |
| *L. schimperi* (Asch. & Klatt) Milne-Redh. | 10 | 47.1 | 6 | 4 | 0 | 2 | 4 | 4 |
| *L. otaviensis* R. C. Foster | 10 | 47.8 | 4 | 6 | 0 | 4 | 4 | 2 |
| *L. bainesii* Baker | 10 | – | 6 | 4 | 0 | – | – | – |
| | 6 | – | 6 | 0 | 0 | 4 | 0 | 2 |
| Subgenus *Lapeirousia* | | | | | | | | |
| Section *Sophronia* | | | | | | | | |
| *L. anceps* (L.f.) Ker Gawl. | ?18 + 2B[1] | – | 2 | 0 | 16 | ←?16→ | | 2 |
| *L. angustifolia* Schltr. | 18 | 27.3 | 2 | 0 | 16 | ←16→ | | 2 |
| *L. pyramidalis* (Lam.) Goldblatt | ca. 18 | 33.1 | 2 | 0 | 16 | ←16→ | | 2 |

TABLE 1. Continued.

| Species | Diploid number | Total chromosome length μm | Karyotype features | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Size | | | Morphology | | |
| | μm | | L | M | S | m | sm | a |
| *L. silenoides* (Jacq.) Ker Gawl. | 18 + 0 − 2B[2] | 27.1 | 2 | 0 | 16 | ←16→ | | 2 |
| *L. verecunda* Goldblatt | 18 | – | 2 | – | 16 | ←16→ | | 2 |
| *L. exilis* Goldblatt | 18 (+ 0 − 2B) | 29.8 | 2 | 0 | 16 | ←16→ | | 2 |
| *L. jacquinii* N. E. Br. | 18 (+ 0 − 2B)[3] | 25.7 | 2 | 0 | 16 | ←16→ | | 2 |
| *L. littoralis* Baker | | | | | | | | |
| subsp. *littoralis* | 16 | – | 2 | 2 | 12 | ←14→ | | 2 |
| subsp. *caudata* (Schinz) Goldblatt | 16 | 32 | 2 | 2 | 12 | ←14→ | | 2 |
| *L. odoratissima* Baker | 16[4] | 31.4 | 2 | 2 | 12 | 2 | 12 | 2 |
| *L. oreogena* Goldblatt | 16 + 0 − 2B[5] | 28.8 | 2 | 2 | 12 | ←14→ | | 2 |
| *L. plicata* (Jacq.) Diels | | | | | | | | |
| subsp. *plicata* | 16 | – | 2 | 2 | 12 | ←14→ | | 2 |
| Section *Lapeirousia* | | | | | | | | |
| *L. arenicola* Schltr. | 16 | 26.4 | 2 | 2 | 12 | ←14→ | | 2 |
| *L. barklyi* Baker | 16 | – | 2 | ←14→ | | ←14→ | | 2 |
| *L. divaricata* N. E. Br. | | | | | | | | |
| subsp. *divaricata* | ?16 + 0 − 6B[6] | – | 2 | ←?14→ | | ←14→ | | 2 |
| subsp. *spinosa* Goldblatt (as subsp. *grandiflora*) | 16 | – | 2 | ←14→ | | ←14→ | | 2 |
| *L. dolomitica* Dinter | | | | | | | | |
| subsp. *dolomitica* | 16 | – | 2 | 4 | 10 | ←14→ | | 2 |
| subsp. *lewisiana* (B. Nord.) Goldblatt | 16 | 34.8 | 2 | 4 | 10 | ←14→ | | 2 |
| *L. fabricii* (D. Delaroche) Ker Gawl. | 16 + 1B | – | 2 | ←14→ | | ←14→ | | 2 |
| *L. violacea* Goldblatt | 16 | – | 2 | ←14→ | | ←14→ | | 2 |

[1] Reported as $2n = 20$ (Goldblatt, 1971, 1990a) but almost certainly $2n = 18 + 2B$—two very small chromosomes are probably B chromosomes.
[2] In light of two counts here of $2n = 18 + 0 - 2B$ for the species, we think the earlier report of $2n = 20$ (Goldblatt, 1990a) should correctly be $2n = 18 + 2B$.
[3] Earlier counts included $2n = 18$, ca. 20 and 18(–20)—these should probably correctly be $2n = 18 + 0 - 2B$.
[4] Two populations reported as having $2n = 18$ probably had $2n = 16 + 2B$.
[5] Earlier counts of $2n$ = ca. 18, 16–18 (Goldblatt, 1971, 1972) probably reflected uncertainty due to the irregular presence of B chromosomes; individuals counted here are from the same extended population as examined before.
[6] Originally reported as $2n$ = ca. 20 and $2n = 20$ (Goldblatt, 1971, 1990a), but we think probably correctly $2n = 16 + 0 - 6B$. Original counts included cells with as few as 16 and as many as 22 chromosomes.

TABLE 2. Genome sizes estimated for selected species of *Lapeirousia* following the classification of Goldblatt (1990). All C-values have been reduced to the 1C level. Measurements were made cytophotometrically by Jane Masterson with *Nicotiana tabaccum* as a standard; values represent the means of 10 measurements.

| Taxon | Mean 2C-value pg | Chromosome number $2n$ | Mean 1C-value pg |
|---|---|---|---|
| *L. erythrantha* | 2.7 | 8 | 1.35 |
| | 5.8 | 12 | 1.45 |
| *L. gracilis* | 2.4 | 12 | 1.20 |
| *L. otaviensis* | 5.09 | 10 | 1.27 |
| *L. schimperi* | 5.08 | 10 | 1.27 |

ulation. Some individuals have four satellites: one pair, on the second longest chromosome pair, are comparatively long, slightly exceeding the short arms in length; a third satellite on chromosome 3 is also fairly large; and a fourth satellite, extremely large, is located on one of the shortest chromosomes, the short arm of which is minute. Other individuals have small satellites on the second chromosome pair (the most common and presumably the basic condition in the genus).

*Prophase morphology.* In all karyotypes one long acrocentric chromosome pair, often the only long pair in the entire complement, has a distinctive prometaphase structure (Fig. 26). Largely heterochromatic and darkly stained, a small subterminal portion of the long arm is euchromatic. So distinctive is its appearance that we assume that this long chromosome pair is homologous across all the species so far examined and that it is maintained intact, whereas some (or possibly all) of the other chromosomes have been involved in structural rearrangements. The small chromosomes, found in the majority of species, are largely heterochromatic except for the distal ends of the longer arms, which are euchromatic and lightly stained until metaphase (Fig. 26). In *Lapeirousia schimperi* and *L. otaviensis* profound structural rearrangement of the karyotype makes identification of the conserved long chromosome pair of most other species difficult, but, at least in *L. schimperi*, the second longest pair seems homologous with the conserved long pair of most other species (Fig. 26F).

*Total chromosome length.* Irrespective of chromosome number, the majority of species of *Lapeirousia* examined have a total chromosome length in the 24–29 μm range (Table 1), which we assume is the diploid level for the genus. Total chromosome length is close to twice this amount in the $2n = 12$ cytotype of *L. erythrantha* (54.1 μm), but not in the $2n = 8$ cytotype of the species (24.5 μm) (Table 2). This doubling is also found in *L. rivularis* (47.2 μm), *L. schimperi* (47.1 μm), and *L. otaviensis* (47.8 μm). We assume this represents cryptic polyploidy (i.e., polyploidization either followed or preceded by descending dysploidy). Absolute DNA amount per genome (Table 2) is available for the two cytotypes of *L. erythrantha* and for *L. gracilis*, *L. otaviensis*, and *L. schimperi*. These determinations confirm the estimates based on total chromosome length. *Lapeirousia otaviensis*, *L. schimperi*, and $2n = 12$ *L. erythrantha* have 5.1–5.8 pg DNA per genome, whereas *L. gracilis* and $2n = 8$ *L. erythrantha* have 2.7–2.8 pg per genome.

Total chromosome length falls some 20–40% above the expected diploid level (Table 1) in a few species (*L. corymbosa*, *L. azurea*, *L. littoralis*, *L. dolomitica*), but we doubt that these species are polyploid because they have karyotypes nearly identical with obviously diploid species. Some other phenomenon must be involved in the increase in total chromosome length in these examples, which seems beyond what might be considered experimental error. *Pillansia templemanii* is obviously tetraploid. Our counts confirm tetraploidy already reported in two other populations (Goldblatt, 1971, 1977) of this fairly narrowly distributed species.

*B chromosomes.* A significant part of the karyotypes of some species, B chromosomes are identified in *Lapeirousia* by precocious and uniform dark staining at prophase. They vary considerably in size, being nearly as long as the long chromosomes in *L. oreogena* (Fig. 22), but more commonly they are about as long as the small chromosomes. All three populations of *L. silenoides* now known cytologically appear to have B chromosomes (Fig. 17), which are also fairly common in the $2n = 12$ cytotype of *L. erythrantha*. We detect no particular geographic or ecological pattern to the distribution of B chromosomes in the genus but note that B chromosomes have so far been identified only in species with higher diploid numbers. Because of their frequency, we have concluded that some past counts in the genus, inconsistent with our current findings, are due to the unrecognized presence of B chromosomes. The presumed correct chromosome numbers are included in Table 1 with footnotes explaining our reasons for assuming past errors.

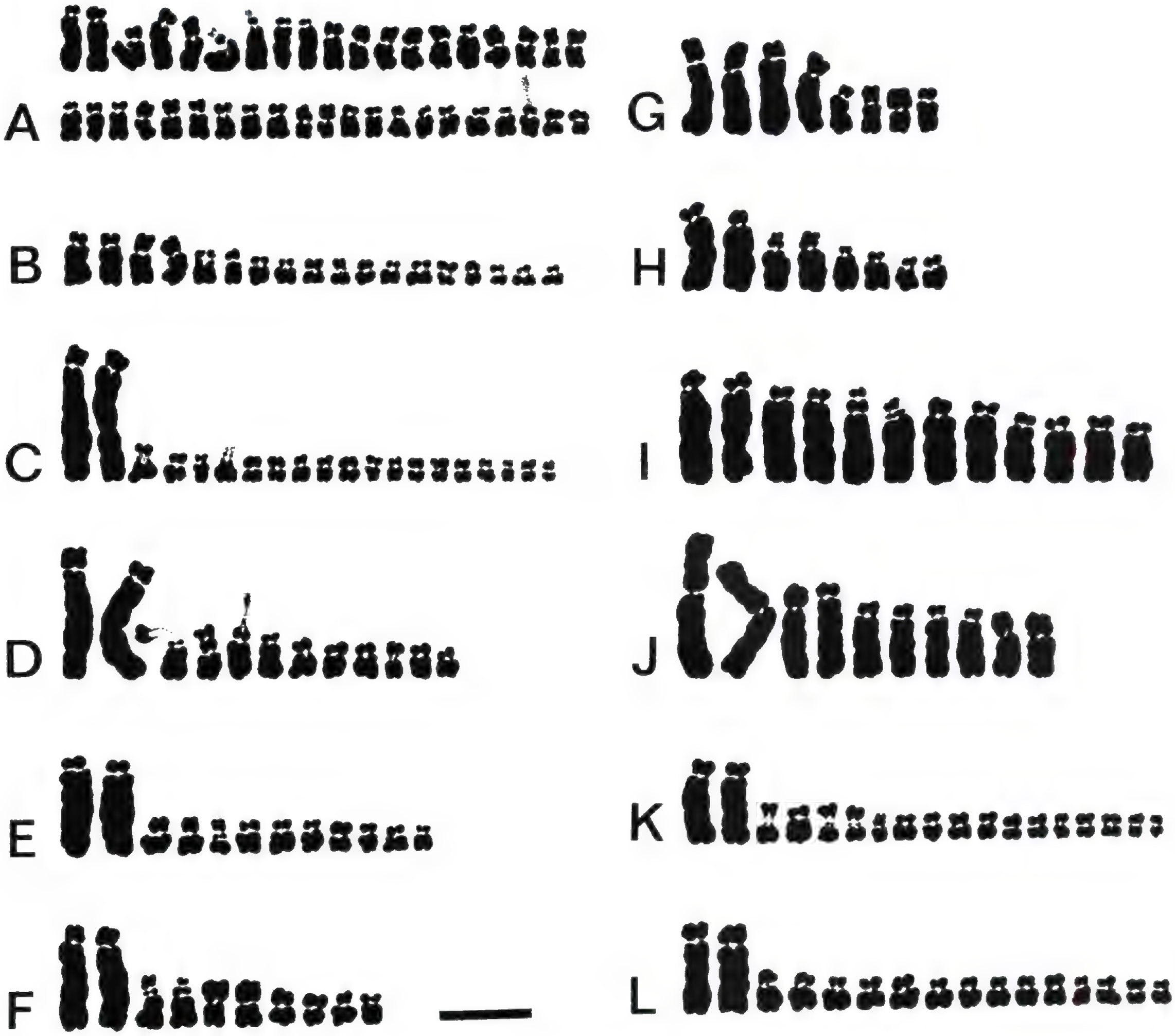



FIGURE 27. Idiograms of karyotypes of *Pillansia*, *Watsonia*, and selected species of *Lapeirousia*.—A. *P. templemanii*.—B. *W. coccinea*. C. *L. azurea* ($2n = 20$).—D. *L. gracilis* ($2n = 12$).—E. *L. neglecta* ($2n = 12$).—F. *L. sandersonii* ($2n = 10$).—G. *L. coerulea* ($2n = 8$).—H. *L. erythrantha* ($2n = 8$).—I. *L. erythrantha* ($2n = 12$).—J. L. schimperi ($2n = 10$).—K. *L. silenoides* ($2n = 18$).—L. *L. odoratissima* ($2n = 16$). Scale bar, 5 μm.

## DISCUSSION

Based both on outgroup comparison, and on the more common trends in numerical change in chromosome number of plants (Jones, 1974, 1977) we infer that the ancestral base number in *Lapeirousia* is most likely $x = 10$. *Lapeirousia* is currently regarded as a member of tribe Watsonieae (subfamily Ixioideae) (Goldblatt, 1989, 1990c, 1991) in which other base numbers are $2n = 20$ (*Thereianthus*, *Micranthus*), 18 (*Watsonia*), and 16 (*Savannosiphon*) (Goldblatt & Marais, 1979; Goldblatt, 1989). *Pillansia*, only genus of Pillansieae, most primitive of the three tribes of Ixioideae, also has $x = 10$ ($2n = 40$) (Goldblatt, 1977), an observation confirmed here for two additional populations of the species. Moderately bimodal karyotypes characterize both *Micranthus* and *Watsonia* (Goldblatt, 1971). The karyotype of *Lapeirousia* differs from that of *Micranthus* largely in its more pronounced bimodality, but the patterns seem comparable. In *Watsonia*, with $2n = 18$, there are two long and seven short chromosome pairs.

Within *Lapeirousia* differences in number and karyotype seem best explained by reduction in number, accomplished by fusion and elimination of redundant centromeres (i.e., unequal reciprocal or Robertsonian translocation, see Jones, 1974,

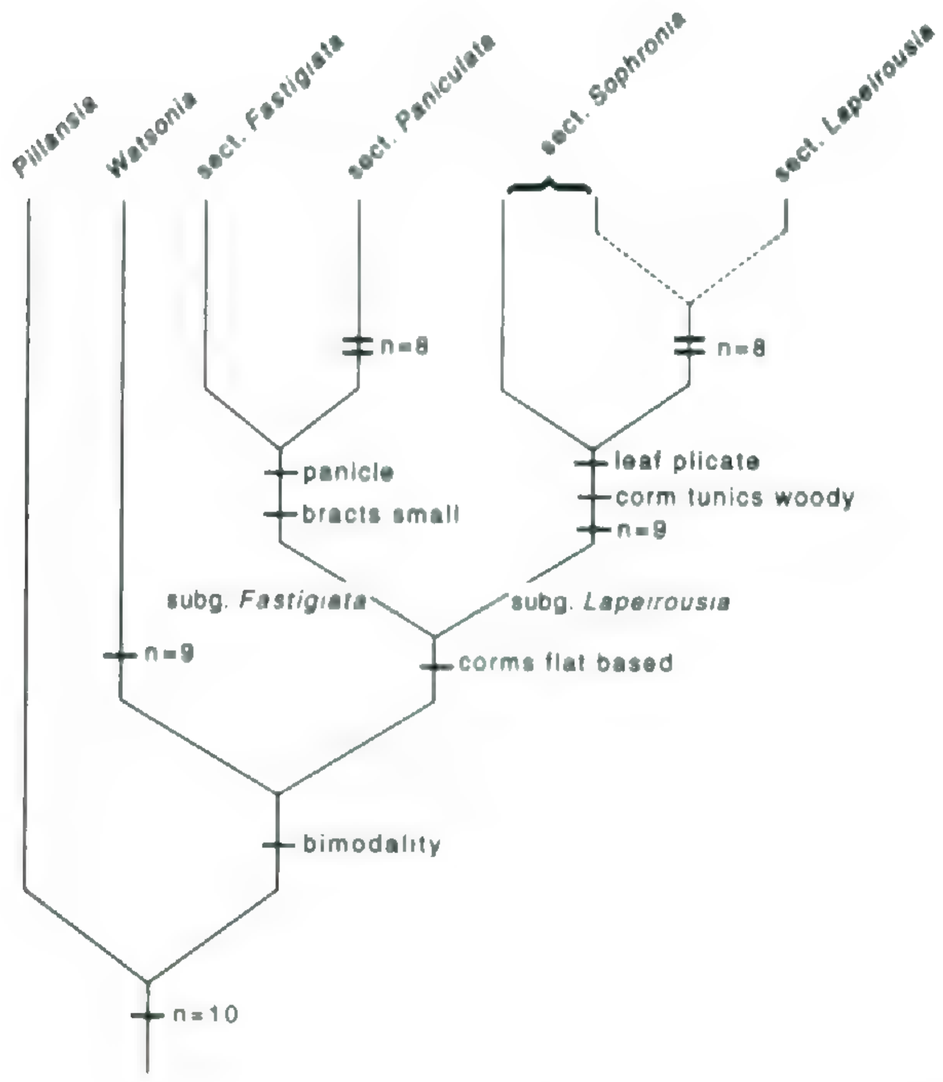



FIGURE 28. Diagram of relationships of *Lapeirousia* and its subgenera and sections, including outgroups *Watsonia* and *Pillansia*, with chromosomal data superimposed on a topology established by Goldblatt and Manning (1990). Although both *Watsonia* and *Lapeirousia* sect. *Lapeirousia* have $n = 9$, they are not homologous characters: the karyotypes indicate independent derivation in each lineage.

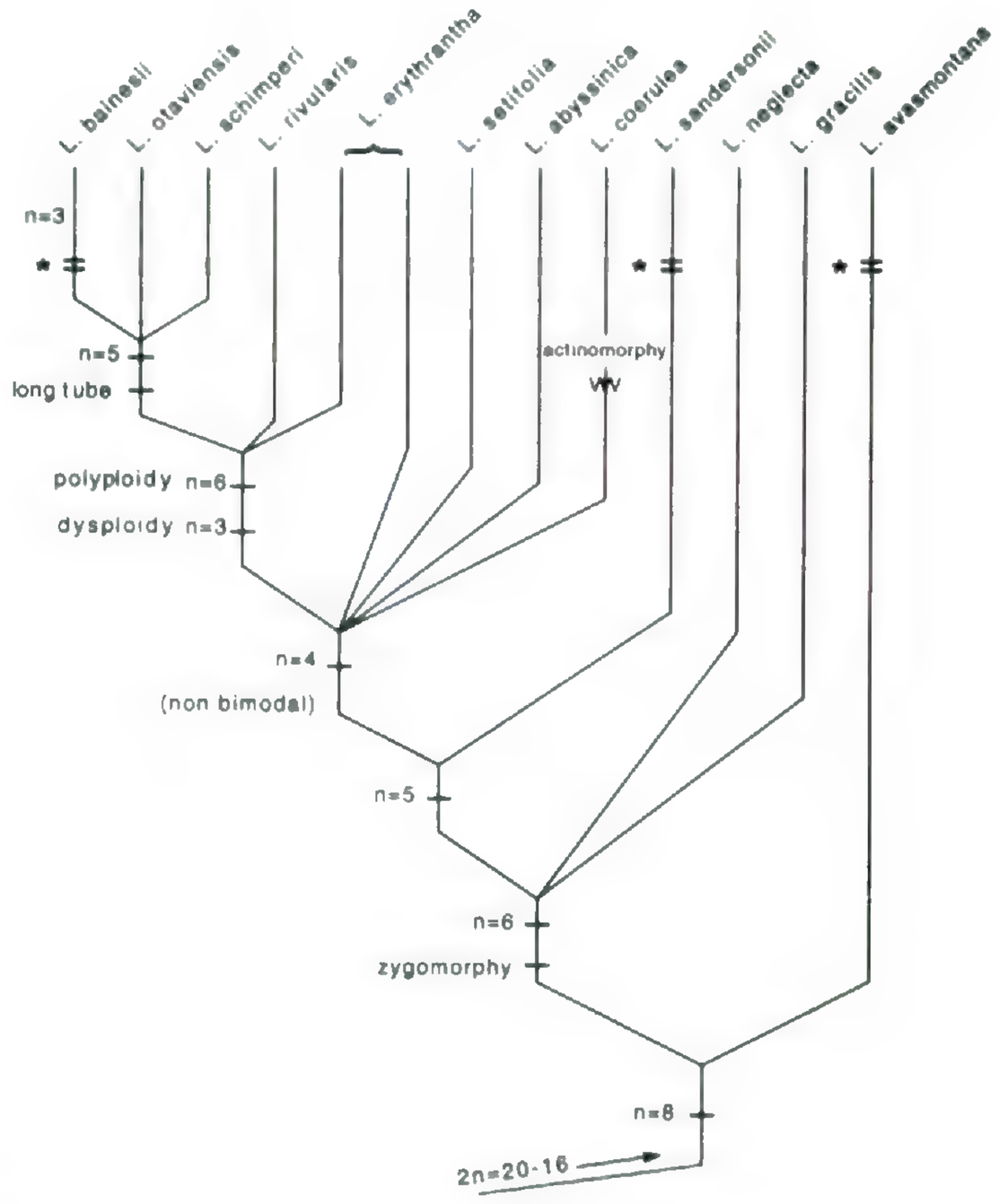



FIGURE 29. Diagram of inferred relationships in *Lapeirousia* sect. *Paniculata*. The tree is based largely on chromosomal characters, but includes apomorphic morphological characters established by Goldblatt (1990a).

1977). This hypothesis is also supported by the observed increase in size of one chromosome pair as number decreases (Table 1).

The infrageneric phylogeny established by Goldblatt and Manning (1990) for *Lapeirousia* makes it clear that decrease in number has occurred in subgenera *Paniculata* and *Lapeirousia* independently (Fig. 28). All species of subgenus *Lapeirousia* have numbers based on $x = 9$ or 8, and the only counts so far obtained for section *Lapeirousia*, excluding B chromosomes, are $2n = 16$, a number also present in some species of section *Sophronia*. It is uncertain at present whether $n = 8$ was achieved more than once in subgenus *Lapeirousia*. Chromosomal data suggest that section *Sophronia* may be paraphyletic with section *Lapeirousia* nested within it. This question awaits further investigation.

In subgenus *Fastigiata*, section *Fastigiata* consistently has $2n = 20$, but the lowest number in section *Paniculata* is $2n = 16$, in *L. avasmontana*, one of two species in the section with actinomorphic flowers (Fig. 29). Among the remaining species of the section relationships are obscure except for a small clade of species with pale-colored flowers with long perianth tubes (*L. schimperi*, *L. otaviensis*, and *L. bainesii*). Phylogeny of the section must therefore be largely inferred from the karyology. Decrease in number appears to have proceeded stepwise with one or more species at each step (Fig. 29), with a plateau at $2n = 8$, where the central species is *L. erythrantha* (previously thought to have exclusively $2n = 12$). *Lapeirousia coerulea*, which also has $2n = 8$, has actinomorphic flowers, almost certainly a reversal, given its nested position within a clade of largely zygomorphic-flowered species.

The situation in *Lapeirousia erythrantha*, with populations having either $2n = 8$ or 12, is particularly interesting. Past counts for the species have consistently been $2n = 12$ (Goldblatt, 1990b), and we have confirmed this count in two additional populations. The $2n = 12$ cytotype is the more widespread, occurring exclusively in Malawi and Zambia, and also in some Zimbabwean populations, but populations with $2n = 8$ are scattered across Zimbabwe and Zaire (Fig. 30). On the basis of total chromosome length, *L. erythrantha*, then only known from its $2n = 12$ cytotype, was assumed to be polyploid, as was *L. rivularis*. We now modify this assumption. Ancestral base number in *L. erythrantha* is most likely $x = 4$, the base number also in the morphologically similar, and presumably closely related, *L. setifolia* and *L. abyssinica* (Goldblatt, 1990b). The $2n = 8$ karyotype of *L. erythrantha* has been confirmed to be diploid, and

the $2n = 12$ karyotype tetraploid by measurement of total DNA genome.

The diploid number of $2n = 12$ may have been achieved by one of two possible paths. Dysploid reduction from $n = 4$ to 3 by Robertsonian translocation followed by tetraploidization to $n = 6$ is one scenario. Alternatively, a polyploid event resulting in tetraploidy, $2n\,(4x) = 16$, and subsequent dysploid reduction to $2n\ (4x) = 12$, may have occurred. We favor the former hypothesis because it involves only two major chromosomal mutations, whereas the second involves three. In *L. erythrantha* polyploidy and subsequent dispersal of the $2n = 12$ cytotype through Zambia, Malawi, and northern Zimbabwe is our best explanation for the cytological pattern now evident in *L. erythrantha*. There seems to be no doubt that the two cytotypes of *L. erythrantha* are conspecific. Except for a slightly more slender growth habit in some of the $2n = 8$ cytotypes, there is nothing we can detect in their morphology to distinguish the cytotype in this common and widespread species.

In *Lapeirousia rivularis*, a similar karyotype, although not identical to the $2n = 12$ cytotype of *L. erythrantha*, is also evidently cryptically polyploid. The origin of this karyotype is uncertain, but it seems to us more parsimonious to assume a derivation from the $2n = 12$ karyotype of *L. erythrantha*. This presumes also the derivation of a species, *L. rivularis*, from a cytotype of *L. erythrantha*. Alternatively, *L. rivularis* may have arisen from other ancestors presumably with $x = 4$ (or 3), with subsequent polyploidization so that the karyotype now resembles that of the $2n = 12$ cytotype of *L. erythrantha*.

Our results indicate that *Lapeirousia schimperi*, *L. otaviensis*, and presumably the related *L. bainesii*, which form a clade (Goldblatt, 1990a) distinguished by their long- to very long-tubed flowers, are also polyploid (Tables 1, 2). We cannot say whether they are more likely to be derived from *L. erythrantha* or to have another ancestry, but parsimony is followed in Figure 29, in the tree generated by combining cytology and morphology of the lineage.

Continuing studies will eventually yield more light on the question of phylogeny of *Lapeirousia*. It is, however, clear that the karyological history of the genus is remarkably complex and has probably involved primary dysploidy in at least two lineages, from $x = 10$ to 8 in subgenus *Lapeirousia*, and from $x = 10$ to 4 in section *Paniculata*. A secondary burst of polyploidy is evident in section *Paniculata*, and secondary descending dysploidy appears to have occurred in *L. erythrantha* (and its close ally *L. rivularis*) and perhaps independently in the clade that includes *L. schimperi*, *L. otaveinsis*, and *L. bainesii*, the latter having populations with $n = 6$.

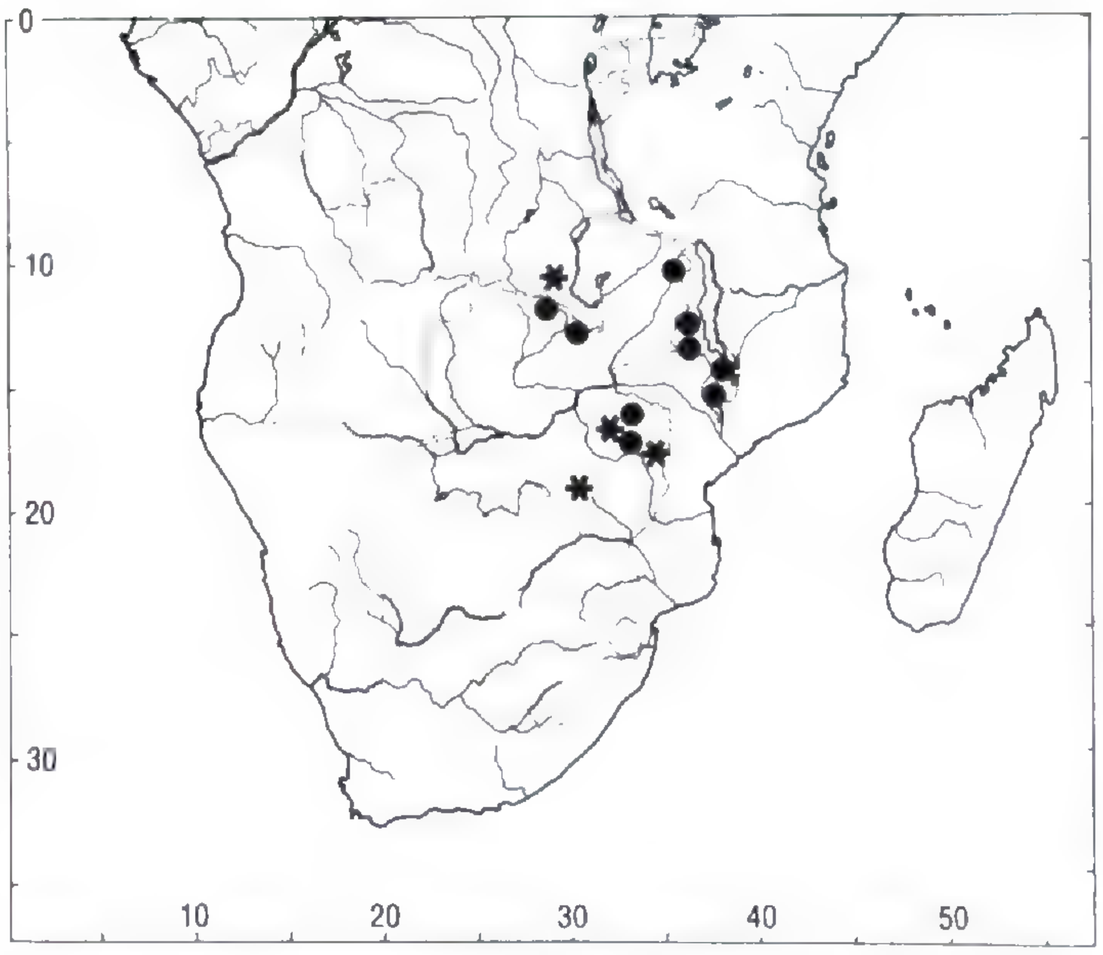



FIGURE 30. Cytogeography of *Lapeirousia erythrantha*. Populations with $2n = 8$ represented by stars; populations with $2n = 12$ by solid circles.

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APPENDIX. New chromosome numbers in *Lapeirousia*, *Pillansia*, and *Watsonia* with collection data. Karyotype details are included in Table 1. Acronyms (abbreviated according to Holmgren et al., 1990) following the collection data refer to the herbaria in which the vouchers are housed. Species are arranged alphabetically within sections.

| Species | Diploid number $2n$ | Collection data |
|---|---|---|
| *Pillansia templemanii* | 40 | South Africa. Cape: Kogelberg, *Bean s.n.* (MO); Palmiet River valley, *Viviers s.n.* (BOL) |
| *Watsonia coccinea* | 18 | South Africa. Cape: *Goldblatt 9055* (MO) |
| *Lapeirousia* | | |
| Subgenus *Paniculata* | | |
| Section *Paniculata* | | |
| *L. erythrantha* | 8 | Zaire. Mine d'Etiole, *Brooks s.n.*, no voucher; Zimbabwe. Dombashawa, *Goldblatt 9086* (MO); north of Rusape, *Goldblatt s.n.* (MO); near Bulawayo, *Goldblatt s.n.*, no voucher |
| | 12 | Zimbabwe. Christon Bank, Mazowe, *Peters s.n.* (MO); Harare, Cleveland Dam, *Goldblatt s.n.*, no voucher. Zambia. Mufulira, *Goldblatt 7575* (MO) |
| *L. gracilis* | 12 | Namibia. Asab, *Goldblatt & Manning 8870* (MO) |
| *L. rivularis* | 12 | Zambia. Lusaka, *Goldblatt 7537* (MO) |
| *L. sandersonii* | 10 | South Africa. Transvaal: Pretoria Hills, *van Wyk s.n.* (MO) |
| *L. neglecta* | 12 | South Africa. Cape: Jonkershoek, *Esterhuysen 36923* (MO) |
| *L. otaviensis* | 10 | Namibia. Otavi Hills, *Goldblatt & Manning 8837* (MO) |
| Section *Fastigiata* | | |
| *L. corymbosa* | 20 | South Africa. Cape: Cape Point Reserve, *Goldblatt s.n.* (MO) |
| *L. azurea* | 20 | South Africa. Cape: Malmesbury, *Goldblatt 8016* (MO) |
| Subgenus *Lapeirousia* | | |
| Section *Sophronia* | | |
| *L. angustifolia* | 18 | South Africa. Cape: Knersvlakte, *Goldblatt & Manning 9127* (MO) |
| *L. exilis* | 18 + 0 − 2B | South Africa. Cape: north of Springbok, *Goldblatt 2649* (MO) |
| *L. jacquinii* | 18 | South Africa. Cape: north of Garies, *Goldblatt & Manning 9135* (MO) |
| *L. silenoides* | 18 + 0 − 2B | South Africa. Cape: Near Steinkopf, *Goldblatt s.n.*, no voucher; south of Kamieskroon, *Goldblatt 9136* (MO) |
| *L. odoratissima* | 16 | Namibia. East of Windhoek, *Goldblatt & Manning 8803* (MO) |
| *L. oreogena* | 16 + 0 − 2B | South Africa. Cape: Nieuwoudtville, *Snijman s.n.* (MO) |
| *L. pyramidalis* | 18 | South Africa. Cape: Olifants R valley, *Goldblatt & Manning 9223* (MO) |
| Section *Lapeirousia* | | |
| *L. arenicola* | 16 | South Africa. Cape: Knersvlakte, *Goldblatt 9145A* (MO) |
| *L. barklyi* | 16 | South Africa. Cape: Anenous Flats, *Goldblatt & Manning 9460* (MO) |
| *L. dolomitica* subsp. *lewisiana* | 16 | South Africa. Cape: near Garies, *Goldblatt & Manning 9198* (MO) |
| *L. violacea* Goldblatt | 16 | South Africa. Cape: Bidouw Valley, *Goldblatt 9197* (MO) |

# CHROMOSOME NUMBERS OF NEOTROPICAL *CASTILLEJA* (SCROPHULARIACEAE: TRIBE PEDICULAREAE) AND THEIR TAXONOMIC IMPLICATIONS[1]

*T. I. Chuang*[2] *and L. R. Heckard*†[3]

## ABSTRACT

Meiotic chromosome numbers in *Castilleja* are reported for 105 collections representing 34 species, mostly from Mexico, with a few from Central America and South America. Chromosome numbers of the following 19 species are reported here for the first time: *C. bryantii*, *C. ecuadorensis*, *C. fissifolia*, *C. fruticosa*, *C. gracilis*, *C. hirsuta*, *C. integrifolia*, *C. irazuensis*, *C. linifolia*, *C. nubigena*, *C. ornata*, *C. ortegae*, *C. purpusii*, *C. roei*, *C. scorzonerifolia*, *C. stenophylla*, *C. talamancensis*, *C. tenuifolia*, and *C. virgata*. Of the 34 species, 24 are exclusively diploid ($n$ = 12); five are tetraploid ($n$ = 24) only; two are octoploid ($n$ = 48) only; three have two or more levels of ploidy ($n$ = 12, 24, and 72). These polyploid species (including *C. aspera*, *C. integrifolia*, and *C. tenuiflora*) are the most troublesome taxonomically and substantiate our contention that polyploidy and hybridization are largely responsible for the complex morphological variation found in *Castilleja*. It is estimated that only 25% of Mexican elements of *Castilleja* (excluding *C. affinis* and *C. subinclusa*) exhibit polyploidy, in contrast to more than 50% polyploidy in western North American representatives. The unusual chromosome number of $n$ = 10 in the closely related *C. gracilis* and *C. tenuifolia* is postulated to be an aneuploid reduction from an $n$ = 12 progenitor. The role of chromosome number, especially polyploidy, in the evolution of *Castilleja* and its taxonomic significance is indicated for individual species.

This paper represents the fourth in a series of reports on chromosome numbers in *Castilleja* (Scrophulariaceae) and is part of our continuing effort to furnish evidence of the significance of polyploidy and accompanying hybridization in forming the complex patterns of variation that characterize the genus. It is also our intention to clarify taxonomic and evolutionary relationships among its members. Our emphasis in this report is on those species occurring in Mexico, Central America, and South America.

*Castilleja* (Indian Paintbrush) comprises over 200 perennial and annual hemiparasitic species. They are almost all American with their heaviest concentration in western North America, where they have been a continual source of extreme taxonomic difficulty, perhaps due partly to the prevalence of weak barriers to natural hybridization and associated polyploidy. Asa Gray's (1862) comment remains discouragingly prophetic: "The species of this genus are most troublesome and unsatisfactory, not only on account of the difficulty of investigating the dried specimens, but also from the variability of the characters which have been relied upon in arranging them, and especially of the calyx."

Heckard (1968) reported chromosome numbers of 54 taxa in *Castilleja*, largely of the Pacific Coast states and Mexico. Heckard & Chuang (1977) reported chromosome numbers of 35 taxa from the Great Basin and Rocky Mountains, and Chuang & Heckard (1982) reported 13 taxa of annual *Orthocarpus* (sects. *Castillejoides* and *Cordylanthoides*) mainly from California, which have recently been merged into *Castilleja* subg. *Colacus* sect. *Oncorhynchus* (Chuang & Heckard, 1991). Our continuing survey of chromosome numbers in the genus in western North America (Heckard,

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1968; Heckard & Chuang, 1977; Chuang & Heckard, 1982; Chuang & Heckard, unpublished data) has shown that more than half of the 100 species counted are polyploid or have a diploid level plus one or more polyploid levels. For example, one species complex, *Castilleja affinis-litoralis*, has a diploid plus five levels of polyploidy from 4*x* to 12*x*. The widespread *C. miniata* of the western United States and Canada has a diploid and four additional levels of polyploidy from 4*x* to 10*x*.

*Castilleja* is represented in Mexico by approximately 55 species, Central America by 9 species, and South America by 12 species, mostly in the Andes. Judging from its richness in species, mainland Mexico, especially the Sierra Madre Occidental, is one of the major centers of diversity for the genus, second only to the western United States. Mexican and Central American *Castilleja* was last treated monographically by Eastwood (1909), who recognized 54 species, 17 of which were described as new. Although her classification is used as a basis for our review and presentation of chromosome numbers, it is evident that there is need for an updated treatment of Mexican *Castilleja* based on the abundant recent collections in the major herbaria in Mexico and the United States, field observation, cytological investigation, and SEM studies of seeds and trichomes. Subsequently, many new species of Mexican, Central American, and South American *Castilleja* were proposed by various authors. Brandegee (1914) described one from Chiapas, Mexico; Standley, three from mainland Mexico (1936, 1940), one from Costa Rica (1938); Standley & Steyermark (1944), one from Guatemala; Pennell, four from Panama (1940), three from Venezuela (1953); Edwin (1970), four from Peru; Crosswhite (1970) and Rzedowski (1975), one each from mainland Mexico; Holmgren, four from Mexico (1976), four from Costa Rica and Panama (1978), and one from Ecuador (Holmgren & Molau, 1984); Moran (1969, Levin & Moran, 1989), two from islands off Baja California; Breedlove & Heckard (1970), one from Sinaloa, Mexico, originally described as the monotypic genus *Gentrya*, which has recently been relegated to subgeneric status in *Castilleja* (Chuang & Heckard, 1991). Most recently, an additional four species were described from mainland Mexico by Nesom (1992b) and another four from Peru by Chuang & Heckard (1992a), the latter included in our newly proposed bee-pollinated subgenus *Colacus*.

There are only a few reports of chromosome numbers of Mexican *Castilleja*, consisting of scattered data on individual species (Beaman et al., 1962; Ward, 1983, 1984; Ward & Spellenberg, 1986) and four of our unpublished counts indicated on herbarium labels, which were listed in Holmgren's (1976, 1978) and Holmgren & Molau's (1984) publications.

## Materials and Methods

Cytological materials were obtained from the wild by various collectors (see Table 1), and fixed in Farmer's solution (3 anhydrous ethanol: 1 glacial acetic acid, v/v). Fixed flower buds were immediately cooled on ice in the field and stored under refrigeration in the laboratory. All counts were made from aceto-carmine squashes of pollen mother cells and observed with a Zeiss phase contrast microscope. Chromosome drawings were made by camera lucida at magnifications of ×2100 and ×2600.

## Results and Discussion

In this contribution we present meiotic chromosome counts of 105 collections, representing 34 species in *Castilleja* from Mexico, Central America, and South America of which 19 species are reported here for the first time. Among the 34 species represented, 24 are exclusively diploid ($n = 12$) and the remaining ten exhibit polyploidy: five (*C. affinis*, *C. integra*, *C. lithospermoides*, *C. ornata*, and *C. subinclusa*) are tetraploid ($n = 24$) only; two (*C. linifolia* and *C. purpusii*) are octoploid ($n = 48$) only; and three (*C. aspera*, *C. integrifolia*, and *C. tenuiflora*) have two or more levels of ploidy ($n = 12$, 24, and 72). The last three polyploid species are the most troublesome taxonomically and substantiate our contention that polyploidy and hybridization are largely responsible for the complex morphological variation found in *Castilleja*. It is estimated that only 25% of Mexican elements of the genus (excluding *C. affinis* and *C. subinclusa*, which are undoubtedly Californian elements) are polyploid, in contrast to more than 50% of western North American representatives. Many more complex species are found in the western United States, where the genus appears to be undergoing an accelerated phase of evolution.

The chromosome number of $n = 10$ is found in two closely related Mexican species, *C. gracilis* and *C. tenuifolia*, in sect. *Epichroma* Benth. (subg. *Castilleja*), although the same number was reported in *C. lineariloba* (Benth.) Chuang & Heckard (Chuang & Heckard, 1982, published as *Orthocarpus linearilobus* Benth.), which has recently been included in subgenus *Colacus* sect. *Oncorhynchus* (Chuang & Heckard, 1991). It is pos-

TABLE 1. Chromosome numbers of neotropical *Castilleja*. Voucher specimens are deposited in the Jepson Herbarium (JEPS) and the University of California Herbarium (UC), both at Berkeley, except where otherwise indicated. First reports for species are in boldface.

*Castilleja affinis* Hook. & Arn. subsp. *affinis*

$n = 24$. MEXICO. BAJA CALIFORNIA: 2 mi. SE of La Misión, N of Ensenada, *Heckard 4070*.

*Castilleja affinis* Hook. & Arn. subsp. *affinis*, aff. *C. subinclusa*

$n = 24$. MEXICO. BAJA CALIFORNIA: 2.5 mi. NW of Ejido Urupan, 8 mi. NW of Santo Tomás, *Heckard 4080*; 2 mi. SW of Rancho Santa Clara, ca. 7 mi. N of San Vicente, *Heckard 4081*.

*Castilleja arvensis* Schltdl. & Cham.

$n = 12$. MEXICO. CHIAPAS: 20 km SE of San Cristóbal de las Casas, *Cruden 1539*.

*Castilleja aspera* Eastwood

$n = 12$. MEXICO. CHIHUAHUA: W of Creel, *Bye 7823*; 3.2 km N of La Mesa del Huracán, *Holmgren 8039* (NY). DURANGO: 14 km W of Río Mimbres, Ruta 40, *Cruden 1301*.

**Castilleja bryantii** Brandegee (Fig. 1)

$n = 12$. MEXICO. BAJA CALIFORNIA: Rancho Saltillo, 60 mi. SE of Villa Constitución, *Heckard 3250*. BAJA CALIFORNIA SUR: Aguaje de San Antonio, Arroyo el Coyote, *Carter 5459*.

**Castilleja ecuadorensis** N. Holmgren (Fig. 2)

$n = 12$. ECUADOR. LOJA: Cuenca–Loja road, 26.2 km N of Saraguro, *Holmgren 10170*.

**Castilleja fissifolia** L. f. (Fig. 3)

$n = 12$. ECUADOR. CARCHI: El Angél–Tulcan road, 6.7 km SW of summit, *Holmgren 10082*. COTOPAXI: Parque Nacional Cotopaxi, 3.9 km up Refugio road, *Holmgren 10105*. PICHINCHA: trail to Volcán Ruca Pichincha, *Holmgren 10126*.

*Castilleja foliolosa* Hook. & Arn.

$n = 12$. MEXICO. BAJA CALIFORNIA: ca. 3 mi. SE of La Misión, N of Ensenada, *Heckard 4072*.

**Castilleja fruticosa** Moran

$n = 12$. MEXICO. BAJA CALIFORNIA: Guadalupe Island, S end mesa E of weather station, *Moran 13768* (SD).

**Castilleja gracilis** Benth. (Fig. 4)

$n = 10$. MEXICO. MICHOACAN: ca. 10 km NW of Tuxpan, *Cruden 1973*.

**Castilleja hirsuta** Martens & Galeotti (Fig. 5)

$n = 12$. MEXICO. VERA CRUZ: ca. 26 km NE of Perote, *Cruden 1709*; ca. 24 km NW of Jalapa, *Cruden 1706*.

*Castilleja integra* A. Gray

$n = 24$. MEXICO. CHIHUAHUA: 14 km SSW of Buenaventura, *Cruden 2014*.

TABLE 1. Continued.

**Castilleja integrifolia** L. f. (Figs. 6, 7, 8)

$n = 12$. MEXICO. CHIAPAS: 13 km SE of Comitán, *Cruden 1552*; ca. 54 km E of Tuxtla, *Cruden 1937*; S end of valley of San Cristóbal, *Breedlove 25280* (CAS).

$n = 24$. GUATEMALA. HUEHUETENANGO: ca. 15 km E of Paquix, *Cruden 1578*. MEXICO. OAXACA: ca. 24 km SSW of Tamazulapan, *Cruden 1434*; road from Oaxaca to Puerto Escondido, 8 km S of Jiquila, *Heckard 4735*. MEXICO: just N of San Bartolo, *Cruden 1352*.

$n = 72$. MEXICO. GUERRERO: Zacatone, close to summit of Cerro Teotepec, *Cruden 1635*; 103 km NW of Puerto El Gallo, *Breedlove 36070* (CAS).

**Castilleja irazuensis** Oersted (Fig. 9)

$n = 12$. COSTA RICA. CARTAGO: Volcán Irazú, *Heckard 6219*.

*Castilleja jiquilpana* Nesom

$n = 12$. MEXICO. MICHOACAN: ca. 13 km W of Jiquilpan, *Cruden 1322*.

*Castilleja lanata* A. Gray

$n = 12$. MEXICO. NUEVO LEON: desert between Matehuela and Doctor Arroyo, *Cruden 1524*. SAN LUIS POTOSI: ca. 23 km E of Ruta 57, *Cruden 1461*; ca. 41 km N of Nunez, *Cruden 1525*.

**Castilleja linifolia** N. Holmgren (Fig. 10)

$n = 48$. MEXICO. DURANGO: 39 mi. N of Estación Coyotes, *Breedlove 18747*; 4 km NW of Los Angeles along road between Mazatlán and Durango, *Breedlove 35738*; ca. 29 km W of El Salto, *Cruden 2000*.

*Castilleja lithospermoides* Kunth

$n = 24$. MEXICO. JALISCO: ca. 18 km S of Autlán, *Cruden 1672*; 4.5 km W of Tizapán el Alto, *Cruden 1320*. NAYARIT: ca. 19 km S of Tepic, *Cruden 1313*.

*Castilleja mexicana* (Hemsl.) A. Gray

$n = 12$. MEXICO. CHIHUAHUA: 13–14 km SSW of Buenaventura, *Cruden 2015*; 6 km NE of intersection of roads to Santa Barbara and Guadalupe y Calvo, *Cruden 2031*. DURANGO: 6.5 km SW of Yerbanis, *Cruden 1849*.

**Castilleja nubigena** Kunth (Fig. 11)

$n = 12$. ECUADOR. COTOPAXI: Parque Nacional Cotopaxi, 6.4 km up the Refugio road, *Holmgren 10101*. NAPO: E side of Laguna Chaloacocha, *Holmgren 10135*.

**Castilleja ornata** Eastwood (Fig. 12)

$n = 24$. MEXICO. CHIHUAHUA: 32.2 km N of La Mesa del Huracán, *Holmgren 8044* (NY).

**Castilleja ortegae** Standley (Fig. 13)

$n = 12$. MEXICO. DURANGO: 17 mi. W of La Ciudad, *Breedlove 18919*. SINALOA: 3.5 mi. W of El Palmito, *Breedlove 16425*; 7

TABLE 1. Continued.

mi. W of Santa Rita, Sierra Surotato, *Breedlove 16520* (CAS); 5 mi. NW of Los Ornos along road to Mocorito, *Breedlove 19192* (CAS).

*Castilleja patriotica* Fernald

*n* = 12. MEXICO. CHIHUAHUA: W of Gonogochic, *Bye 7900*; ejido de San Ignacio, *Bye 7998*; Municipio de Cuauhtémoc, Ruta 16 near K 122, *Bye 7705*; ½ km SW of Cusarare, *Bye 7907*; 19.3 km SSW of La Mesa del Huracán, *Holmgren 8034* (NY).

**Castilleja purpusii** Brandegee

*n* = 48+. MEXICO. MEXICO: Tlamacas, N slope of Popocatépetl, *Cruden 1624*.

**Castilleja roei** Crosswhite (Fig. 14)

*n* = 12. MEXICO. DURANGO: ca. 29 km SW of La Ciudad, *Cruden 1168*; ca. 18 km SW of La Ciudad, *Cruden 1308*; ca. 20 km SW of La Ciudad, *Cruden 1312*. SINALOA: 3 km NE of El Palmito, *Breedlove 36449* (CAS).

*Castilleja saltensis* Eastwood

*n* = 12. MEXICO. DURANGO: 6 mi. W of La Ciudad, *Breedlove 18867*; ca. 8 km W of El Salto, *Cruden 1305*.

*Castilleja schaffneri* Hemsley

*n* = 12. MEXICO. MEXICO: ca. 1 km SW of Sultepec, *Cruden 1659*; Llano Grande, 54 km E of México City, *Cruden 1451*; ca. 2 km E of Santa María del Monte on road to Valle de Bravo, *Cruden 1355*.

**Castilleja scorzonerifolia** Kunth (Fig. 15)

*n* = 12. MEXICO. DURANGO: 9.7 km W of Durango, *Holmgren 8059* (NY); Ruta 45, ca. 32 km SE Ruta 40, *Cruden 1832*. GUERRERO: SW of Xochipala, *Cruden 1628*. JALISCO: ca. 15 km W of Guadalajara, *Cruden 1316*. MEXICO: ca. 6 km N of Atlacomulco, *Cruden 1800*. OAXACA: ca. 20 km N of Ixtlán de Juárez, *Cruden 1388*. SAN LUIS POTOSI: Ruta 40, K 230–231, ca. 34 km W of Ruta 57, *Cruden 1463*.

**Castilleja stenophylla** M. E. Jones (Fig. 16)

*n* = 12. MEXICO. CHIHUAHUA: W of Creel, *Bye 7472*; ca. 18 mi. S of La Junta along road to San Juanito, *Bye 7650*; N of Humira, *Bye 7871*; ejido de San Ignacio Arareco, N of church, *Bye 7881*; ejido de San Ignacio, S of Creel air-strip, *Bye 7999*; S of Laguna de Bavicora, *Holmgren 8017* (NY); 103.5 km SW of Hidalgo del Parral, *Holmgren 8047* (NY).

*Castilleja subinclusa* Greene subsp. *subinclusa*

*n* = 24. MEXICO. BAJA CALIFORNIA: ca. 14 mi. E of Ensenada, *Heckard 4078*; 2 mi. NE of Meling Ranch, *Heckard 4085*; 6 mi. W of Meling Ranch, *Heckard 4087*.

TABLE 1. Continued.

**Castilleja talamancensis** N. Holmgren (Fig. 17)

*n* = 12. COSTA RICA. CARTAGO: Cordillera de Talamanca, páramo, *Heckard 6219A*.

*Castilleja tapeinoclada* Loesener (Fig. 18)

*n* = 12. GUATEMALA. HUEHUETENANGO: ca. 19 km E of Paquix, *Cruden 1584*.

*Castilleja tenuiflora* Benth. (Fig. 19)

*n* = 12. MEXICO. COAHUILA: ca. 30 km SE of Saltillo, *Cruden 1685*. DURANGO: 16.3 km WNW of Sombrerete, *Holmgren 8074* (NY). HIDALGO: Parque Nacional El Chico, ca. 13 km N Ruta 105, *Cruden 1482*. JALISCO: 3 mi. W of Tizapán El Alto, *Breedlove 18680*. MICHOACAN: 3 mi. SE of Quiroga, *Breedlove 18708*; 3 km NW of Comanja, *Cruden 1334*. MORELOS: on road from Tres Marias, 5 km below Zempoala, *Dempster 4378*. NUEVO LEON: ca. 2 km E of Iturbide, *Cruden 1520*. OAXACA: 21 km NE of Oaxaca, *Cruden 1604*; Rancheria El Tejocote, Santiago Tenango, *Heckard 4722*. ZACATECAS: 15 mi. N of Sombrerete, *Breedlove 18723*.

*n* = 24. MEXICO. CHIHUAHUA: on N side of Barranca de Batopilas, *Bye 7779*. DURANGO: 46 mi. N of Estación Coyotes, *Breedlove 18776*; 17 mi. W of La Ciudad, *Breedlove 18914*. MEXICO: 18 km NW of Santa María de Monte on road to Valle de Bravo, *Cruden 1353*. PUEBLA: 3 km SW of Puebla–Veracruz state line, *Cruden 1394*. SINALOA: Canyon de Tarahumares, Sierra Surotato, *Breedlove 19280* (CAS).

**Castilleja tenuifolia** Martens & Galeotti (Fig. 20)

*n* = 10. MEXICO. MEXICO: 14 km SW of Villa Guerrero, *Cruden 1796*. MICHOACAN: ca. 10 km E of Morelia, *Cruden 1977*; ca. 10 km NW of Tuxpan, *Cruden 1972*; 3 mi. SE of Quiroga, *Breedlove 18706*; ca. 26 km W of Jiquilpan, *Cruden 1229*.

**Castilleja virgata** (Wedd.) Edwin (Fig. 21)

*n* = 12. ECUADOR. TUNGURAHUA: Ambato–Guaranda road on N flank of Volcán Chimborazo, *Holmgren 10142*.

tulated that $n = 10$ may be derived from an aneuploid reduction from $n = 12$ progenitors, and is apparently of independent origin in these two subgenera.

Knowledge of basic chromosome number and range of polyploidy has helped in understanding the causes of taxonomic complexity in this genus. Nonetheless, this information alone does not provide sufficient evidence for making taxonomic judgments at the subgeneric, sectional, and specific levels, because of chromosomal constancy at the

diploid level (except $n = 10$ in the three species mentioned above) and abundant intraspecific polyploidy. We believe that extensive field observation of variation patterns and additional SEM studies of seeds and trichomes remain the best source of evidence for such taxonomic decisions. Overemphasis of minor morphological variation, especially in complex polyploid species, may lead to unwieldy and impractical classification in *Castilleja*.

The annotated list of chromosome numbers including locality and voucher citation is shown in Table 1. When pertinent, we comment on the relationship of chromosome number and hybridization to the evolution and systematics of the genus.

**Castilleja affinis** Hook. & Arn.

*Castilleja affinis* is a widespread polymorphic species, ranging from coastal northern Oregon south to northern Baja California. This is a highly unwieldy complex with six ploidy levels, $n = 12$ to 72 (Heckard, 1968; Chuang & Heckard, unpublished data). This species has been treated recently by Chuang & Heckard (1992b) as comprising three subspecies, namely, subsp. *affinis*, subsp. *neglecta*, and subsp. *litoralis*. Some populations appear to intergrade to such an extent with abutting *C. applegatei* subsp. *pinetorum*, *C. mollis*, *C. subinclusa*, and *C. wightii* that it is difficult to separate them taxonomically. All three counts from Baja California are tetraploid ($n = 24$); this same number is also fairly widely distributed northward to coastal and Sierra Nevada foothill areas of central California (Heckard, 1968; Chuang & Heckard, unpublished data). Undoubtedly, hybridization and polyploidy have played important roles in creating taxonomic perplexity in this species complex. We suspect that the varying combinations of ploidy levels have evolved to ensure that sympatric populations will have different chromosome numbers and thus be able to coexist without freely hybridizing.

**Castilleja arvensis** Schltdl. & Cham.

This annual *Castilleja* is the most widespread species in the genus, extending from central and northeastern Mexico, south to Central America, and nearly through South America. Our count of $n = 12$ agrees with previous reports (Heckard, 1968; Spellenberg, 1986).

**Castilleja aspera** Eastwood

This species of Chihuahua and Durango is variable with regard to herbage and galea indumentum and leaf shape, but is generally recognizable by the shallowly cleft lateral calyx lobes with acute segments. The chromosome numbers of $n = 12$ and 24 have been reported from Durango (Heckard, 1968). We report two additional counts of $n = 12$ from Chihuahua and Durango. Nesom (1992b) described *C. durangensis* based on Cruden's collection (*Cruden 1160*, holotype, TEX; isotypes, GH, UC; reported as *C. aspera*, $n = 12$ by Heckard, 1968) from about 5 km northeast of El Salto, Durango. We regard these as minor morphological differences of little taxonomic significance at the specific level. The plants may be forms intermediate between *C. aspera* and *C. scorzonerifolia*; nevertheless, this morphological variation deserves further critical study in the field.

**Castilleja bryantii** Brandegee

This species, endemic to Baja California and extending from the vicinity of San Ignacio to the Cape Region, is reported here for the first time as $n = 12$. *Castilleja socorrensis*, a species closely related to *C. bryantii* and endemic to Isla Socorro, was recently proposed by Moran (Levin & Moran, 1989) and was said to differ from the latter mainly by its smaller flowers. Whether these two should be regarded as separate species must await further study.

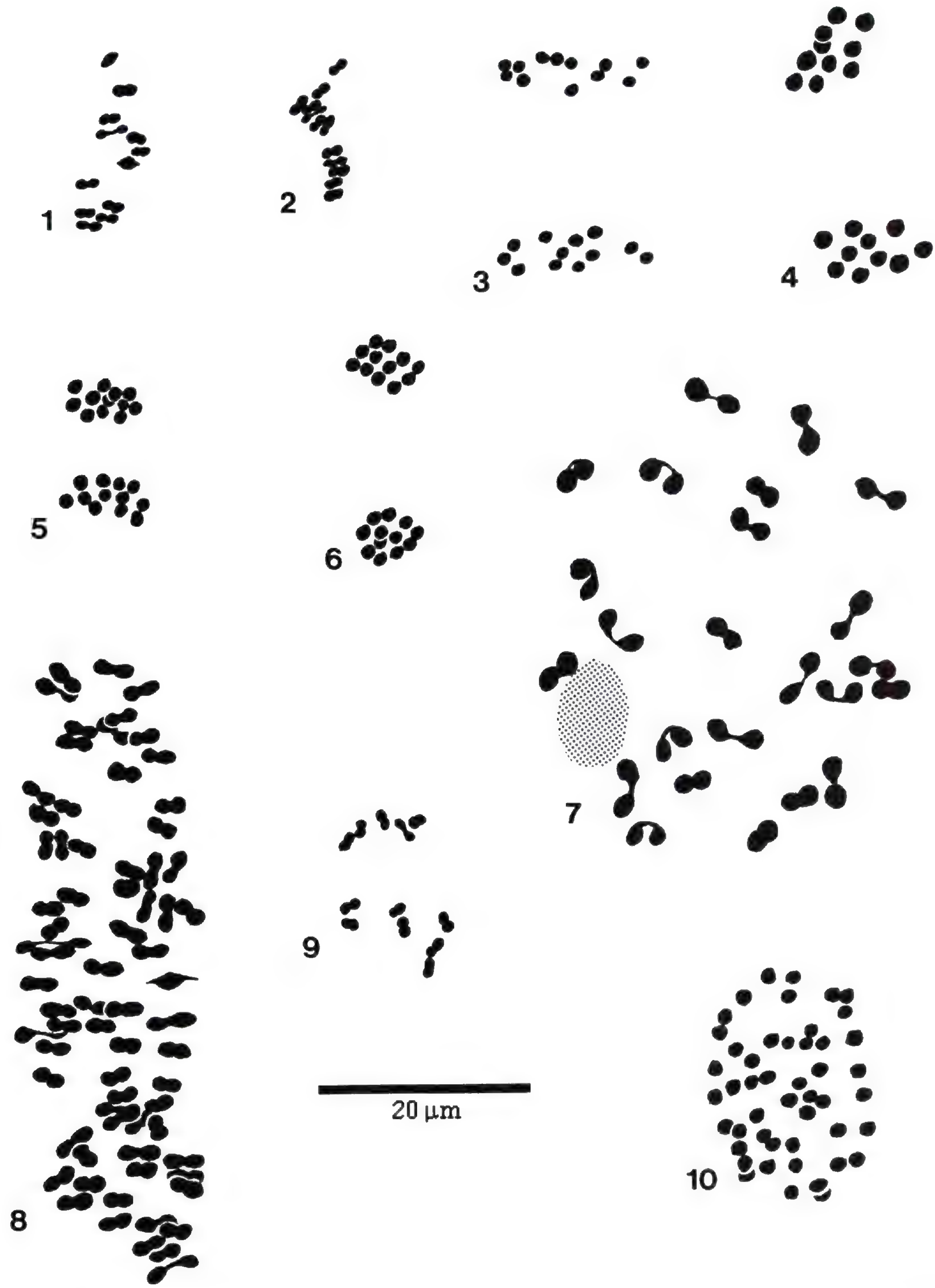
**Castilleja ecuadorensis** N. Holmgren

This species, endemic to Ecuador, is perhaps a close relative of the highly variable *C. fissifolia*. The count of $n = 12$ represents the first report for this species.

**Castilleja fissifolia** L. f.

*Castilleja fissifolia*, the lectotype species of the genus, appears to be an exceptionally polymorphic species with regard to habit and leaf division, and many forms have been accorded separate specific rank. Based on his own observations, Weddell (1857) concluded that intergradations occur between different growth forms, as well as different developmental forms of calyx, corolla, and leaves, and treated these as varieties of a single species, including even *C. integrifolia*. Melchior (1931) followed this disposition, but raised Weddell's varieties of *C. fissifolia* to subspecific level. This species complex awaits a comprehensive investigation over its entire range of distribution to determine whether these morphological forms deserve taxonomic recognition and at what rank.

Our count of $n = 12$ from Ecuador (three populations) represents the first number reported for




FIGURES 1–10. Meiotic chromosome figures of first counts of Mexican, Central American *Castilleja*. The stage of meiosis for each phase is indicated as: Diak., diakinesis; MI, metaphase I; TI, telophase I; TII, telophase II. —1. *C. bryantii*, $n = 12$, MI (*Heckard 3250*). 2. *C. ecuadorensis*, $n = 12$, MI (*Holmgren 10170*).—3. *C. fissifolia*, $n = 12$, TI (*Holmgren 10105*).—4. *C. gracilis*, $n = 10$, TI (*Cruden 1973*). —5. *C. hirsuta*, $n = 12$, TI (*Cruden 1709*).—6. *C. integrifolia*, $n = 12$, 1/2 portion of TII (*Cruden 1552*).—7. *C. integrifolia*, $n = 24$, Diak. (*Cruden 1352*).—8. *C. integrifolia*, $n = 72$, MI (*Cruden 1635*).—9. *C. irazuensis*, $n = 12$, Diak. (*Heckard 6219*).—10. *C. linifolia*, $n = 48$, 1/2 portion of TI (*Breedlove 18747*).

this species, although our unpublished number was listed in Holmgren & Molau's (1984) treatment of Ecuadorian Scrophulariaceae.

**Castilleja foliolosa** Hook. & Arn.

This species, one of the most distinct in cismontane California and northern Baja California, is easily separable by its herbage densely covered with white-woolly branched hairs, undivided lateral calyx lobes, and tight-fitting seed coat. This count of $n = 12$ from northern Baja California agrees with a previous report (Heckard, 1968). The total of seven populations sampled thus far has given only diploid counts.

**Castilleja fruticosa** Moran

*Castilleja fruticosa* is endemic to the southern end of Guadalupe Island, Mexico, and is a close relative of the little known *C. guadalupensis* Brandegee, another endemic to Guadalupe Island, but occurring in a different habitat on the higher and much moister northern part of the island. Moran (1969) pointed out, "It (*C. guadalupensis*) has not been collected since 1898 and evidently is now very rare if not extinct." This species is distinguished from *C. guadalupensis* by its herbage and bracts covered with glandular hairs intermixed with pilose, longer nonglandular hairs, in contrast to the densely and closely tomentose dendritic hairs of the latter. Our count of $n = 12$ is the first number reported for this species.

**Castilleja gracilis** Benth.

The count of $n = 10$ represents the first report for this species, although Holmgren (1976) indicated our unpublished count on the herbarium label. This species is closely related to *C. tenuifolia*, which has the same chromosome number of $n = 10$, but has a larger stature, a longer corolla, and a much more colorful calyx. *Castilleja venusta* Rzedowski (1975), described from Cerro Teotepec, Guerrero, Mexico, resembles *C. gracilis* in vegetative morphology. However, a careful study of an isotype of *C. venusta* (*Rzedowski 18150*, MICH) reveals that it has distinct floral features in its well developed 3-lobed lower corolla lip and truncate calyx lobes. It would be interesting to see whether *C. venusta* also has the same chromosome number of $n = 10$ as found in *C. gracilis* and *C. tenuifolia*.

**Castilleja hirsuta** Martens & Galeotti

Chromosome counts of $n = 12$ were determined from two populations, both from Veracruz, and represent the first reports for this species. This species occurs in Morelos, Hidalgo, and Veracruz and is distinguishable by its entire calyx lobes, which are dilated distally and colored deep-red down to a near-ovary position. Bentham (1846) treated this species in sect. *Epichroma* Benth. on the basis of the somewhat enlarged calyx-limb. We would agree with Eastwood (1909) in including it in sect. *Euchroma* (Nutt.) Benth. because of the spicate inflorescence, entire and nearly orbicular to oblong-lanceolate leaves, and a calyx subequally cleft in front and in back. It is perhaps related to *C. scorzonerifolia*, but this possibility needs further study.

**Castilleja integra** A. Gray

This fairly well defined species is widespread from northern Mexico (Nuevo León, Coahuila, Durango, Chihuahua, and Sonora) north to the southeastern and southwestern United States. It is one of the Mexican elements of *Castilleja* that extends north to the adjacent regions in the United States. This species is closely related to *C. purpurea* and the newly described *C. genevievana* (Nesom, 1992a), but is distinguished by its entire leaves and mostly orange-red to scarlet inflorescence. Because of its intermediate morphology and range of distribution between *C. integra* and *C. purpurea*, *C. genevievana* may represent a form intermediate between the two.

Two chromosome levels ($n = 12$ and 24) were previously reported for 15 populations from our samples (Heckard, 1968; Heckard & Chuang, 1977) and two collections by Ward (1983, 1984). No cytogeographic pattern is apparent in the distribution of the two cytotypes in the United States. The count of $n = 24$ here represents the first count for this species from Mexico. More sampling throughout the range of the species, particularly from Mexico, is needed to establish its cytogeographic patterns.

**Castilleja integrifolia** L. f.

This species is characterized by its racemose inflorescence, entire leaves, entire floral bracts, and conspicuously falcately spreading flowers, which turn black in drying. It is one of the most widely ranging species in the genus, extending from Colombia north to Central America and southern Mexico. It is highly variable with respect to habit, indumentum, leaf shape and size, and color of bracts and flowers; a few morphological variants have been accorded rank as separate species. It

was relegated to infraspecific rank under *C. fissifolia* by Weddell (1857) and Melchior (1931).

This is one of the few polyploid complexes heretofore found in Mexico, as evident in the newly reported counts of $n = 12$, 24, and 72 for this species. Among the nine chromosome counts obtained thus far, the number $n = 12$ is found in three populations from Chiapas, Mexico; $n = 72$ from two populations in Guerrero, Mexico; and $n = 24$ from four populations in Guatemala. Many more population samplings are needed to establish its cytogeographic patterns. The presence of four levels of chromosome number ($n = 12$, 24, and 72, including $n = 48$ for *C. linifolia*), as well as possible hybridization with the related *C. tenuiflora* and others, are responsible for a large part of the complexity of this species.

The diploid Breedlove collection from a marshy area at the southern end of the valley of San Cristóbal in Chiapas deserves comment. It appears to be an extreme form of *C. integrifolia* in having sparsely puberulent herbage, linear leaves, and narrow flowers. It is also very similar to *C. linifolia* in sharing such features as a racemose inflorescence and linear leaves.

**Castilleja irazuensis** Oersted

This species is narrowly endemic to the summits of the two high volcanoes, Volcán Irazú and Volcán Turrialba, Costa Rica. According to Holmgren (1978), *C. irazuensis* is closely related to *C. talamancensis*, which is endemic to the Cordillera de Talamanca in southern Costa Rica. This report of $n = 12$ represents the first count for this species.

**Castilleja jiquilpana** Nesom

This newly described species (Nesom, 1992b) is endemic to the vicinity of Jiquilpan, and is undoubtedly a close relative of the highly polymorphic *C. scorzonerifolia*. It may be distinguished with some difficulty by its deeply divided leaves with linear lobes and smaller (1 mm long), ovoid-deltoid seeds with a fairly deep-netted seed coat.

This count of $n = 12$ agrees with a previous count from a collection made by Cruden (*Cruden 1149*, ca. 22 km W of Jiquilpan, UC) and published as *C. glandulosa* (Heckard, 1968).

**Castilleja lanata** A. Gray

The count of $n = 12$ from three collections agrees with the one previously reported for this species from New Mexico (Ward, 1983). This species is widespread from northern Mexico (including northern Baja California) and western Texas to southern Arizona, and the northern Channel Islands of California. This is one of the Mexican elements of *Castilleja*, extending north to the southern United States. *Castilleja lanata*, *C. hololeuca* (relegated to subspecific status, Chuang & Heckard, 1992b), together with *C. foliosa* and *C. grisea*, have been included in sect. *Lanatae* (Pennell, 1951) because of their grayish or white-tomentose herbage, branched hairs, and calyx lobes that are rounded or wholly united laterally. This species differs from the closely related *C. foliolosa* and *C. grisea* by its white-woolly felt of long interwoven, slightly branched hairs and entire leaves.

**Castilleja linifolia** N. Holmgren

The count of $n = 48$ (octoploid) from three collections represents the first chromosome number reported for this species, although Holmgren (1976) included this number (in *Cruden 2000* and *Breedlove 18747*) in his original description from our unpublished counts on the herbarium labels. This species is known only from southern Durango and adjacent Sinaloa, and appears to be related to a highly variable polyploid species, *C. integrifolia*, except that the former has glabrous to sparsely pilose herbage, and entire, linear-filiform leaves. It is probable that this octoploid ($n = 48$) is a part of the *C. integrifolia* complex, of which three chromosome levels ($n = 12$, 24, and 72) have thus far been revealed.

**Castilleja lithospermoides** Kunth

The count of $n = 24$ from three populations reported here agrees with a previous report (Heckard, 1968). The identification of these collections appears questionable. Nevertheless, all of them match well a specimen cited by Eastwood (1909) as *C. lithospermoides* (*Pringle 2565*, near Guadalajara, Jalisco, Mexico, UC), in having herbage covered with hispid-pilose nonglandular hairs intermixed with short glandular hairs, and seeds 1.8–2 mm long, linear-oblong, with a shallowly reticulate seed-coat with the membranaceous inner tangential walls of seed-coat cells retained at maturity.

Nesom (1992b) reduced this species to synonymy under *C. scorzonerifolia*, based upon study of microfiche of the types (P). We agree with Nesom that the original illustrations (Kunth, 1817) of *C. lithospermoides* (pl. CLXIV) and *C. scorzonerifolia* (pl. CLXV) are almost identical. Based on specimens at hand, we are able to distinguish four different seed forms among the plants, which we tentatively identify as *C. lithospermoides* and

its close relatives *C. scorzonerifolia*, *C. glandulosa*, and *C. jiquilpana*. We herein designate these four species as the *C. scorzonerifolia* complex, which merits further investigation, especially a careful study of the type specimens as well as field investigation of natural populations over their range of distribution.

**Castilleja mexicana** (Hemsl.) A. Gray

This report of $n = 12$ from three collections agrees with the one previously reported count (Ward, 1984). This species was originally described as *Orthocarpus mexicanus* (Hemsley, 1882: 463) and was meticulously and beautifully illustrated (pl. LXIII. A. figs. 1–6). In his original description, Hemsley commented that, "Although this is very closely allied to *Castilleja sessiliflora*, we have preferred placing it in *Orthocarpus*, because it certainly ought to go into the same genus as *Orthocarpus australis* [= *Castilleja laciniata* Hook. & Arn. from Peru; see Chuang & Heckard, 1991: 657], and because it differs from nearly all the species referred to *Castilleja* in the bifid lobes of the calyx, and in the long exserted corolla with nearly equal lips." This observation substantiates our recent realignment (Chuang & Heckard, 1991) to include Keck's (1927) *Orthocarpus* sects. *Castillejoides* and *Cordylanthoides* in genus *Castilleja* (subg. *Colacus* sect. *Oncorhynchus*).

Eastwood (1909: 583) observed that, "*Castilleja sessiliflora* Pursh is excluded as all specimens seen appear to be *C. mexicana*. The two are very closely related." Nesom (1992a) reduced *C. tortifolia* Pennell to synonymy under *C. mexicana*, but maintained *C. mexicana* and *C. sessiliflora* as distinct species, based on such minor differences as color of bracts and indumentum of stems.

*Castilleja mexicana* and *C. sessiliflora* can easily be distinguished from other Mexican species by their dwarf stature, falcate yellow or purplish corolla long-exserted from the calyx, and well developed lower corolla lip with three thin petaloid lobes nearly equaling the upper lip. These two were included in section *Callichroma* [type: *C. purpurea* (Nutt.) Don] by Bentham (1846); later, Pennell (1935) proposed section *Anthochroma* to include *C. sessiliflora* and its relatives.

**Castilleja nubigena** Kunth

The count of $n = 12$ from two populations is reported here for the first time for this endemic of the high mountains of Ecuador. This species is closely related to *C. pumila* (Benth.) Weddell ex Herrera, and both are perhaps part of the *C. fissifolia* complex. As indicated earlier, Melchior (1931) followed Weddell (1857) in treating most South American species of *Castilleja* as infraspecific taxa under *C. fissifolia*, including this one as *C. fissifolia* subsp. *nubigena* (Kunth) Melchior.

**Castilleja ornata** Eastwood

This count of $n = 24$ is the first report for this species. According to Eastwood (1909), this species is related to *C. glandulosa* (= *C. scorzonerifolia*) in the trisaccate lower lip with the divisions separated by the folds forming the three sacs below, and has different pubescence and generally obtuse leaves.

**Castilleja ortegae** Standley

The count of $n = 12$ from four collections represents the first reported chromosome number for this species. It is distinguished by its narrow, entire, often reflexed leaves, secund racemose inflorescence, distally dilated calyx lobes, and shorter upper corolla lip (beak). Holmgren (1976) created the *Ortegae* group to include this species and *C. pterocaulon* N. Holmgren. Undoubtedly they are closely related to *C. gracilis*, *C. roei*, and *C. tenuifolia* in sect. *Epichroma* Benth., except that the latter three species all have filiform, pinnately dissected leaves. Further study may suggest that *C. ortegae* and *C. pterocaulon* should also be included in this section. *Castilleja ortegae* is found from northern Sonora and southwestern Chihuahua to Sinaloa and adjacent Durango.

**Castilleja patriotica** Fernald

This report of $n = 12$ from five collections in Chihuahua, Mexico, is consistent with previously reported counts from Arizona (Heckard & Chuang, 1977; Ward & Spellenberg, 1986). *Castilleja patriotica* is characterized by its pinnately 3–5-lobed leaves, racemose not secund inflorescence, longer upper corolla lip, and calyx cleft to almost ⅔ in front. It is a member of sect. *Castilleja* (= sect. *Hemichroma* Benth.), which contains *C. fissifolia* (the type of the genus) and *C. integrifolia* of South America, and *C. linariifolia* and *C. subinclusa* (including *C. franciscana*) of the western United States. Holmgren (1976) proposed the designation *Tenuiflorae* group to include *C. patriotica*, *C. tenuiflora*, *C. linifolia*, and *C. mcvaughii* N. Holmgren, based on such features as the narrow, entire, often reflexed leaves, and a long galea equaling or exceeding the tube in length.

FIGURES 11–21. Meiotic chromosome figures of first counts (except *C. tapeinoclada*) of Mexican, Central American, and South American *Castilleja*. The stage of meiosis for each phase is indicated as: Diak., diakinesis; MI, metaphase I; TI, telophase I; TII, telophase II.—11. *C. nubigena*, $n = 12$, TI (*Holmgren 10101*).—12. *C. ornata*, $n = 24$, TI (*Holmgren 8044*).—13. *C. ortegae*, $n = 12$, 1/2 portion of TII (*Breedlove 19192*).—14. *C. roei*, $n = 12$, Diak. (*Cruden 1312*).—15. *C. scorzonerifolia*, $n = 12$, TI (*Holmgren 8059*).—16. *C. stenophylla*, $n = 12$, Diak. (*Holmgren 8017*).—17. *C. talamancensis*, $n = 12$, TI (*Heckard 6219A*).—18. *C. tapeinoclada*, $n = 12$, 1/2 portion of TII (*Cruden 1584*).—19. *C. tenuiflora*, $n = 12$, TI (*Breedlove 18723*).—20. *C. tenuifolia*, $n = 10$, TI (*Cruden 1977*).—21. *C. virgata*, $n = 12$, TI (*Holmgren 10142*).

**Castilleja purpusii** Brandegee

This report of $n = 48+$ is one of the few high polyploid species counted for Mexican *Castilleja* and represents the first estimated number for this species. Although no meiotic irregularity was found, it was impossible to make an accurate count because of the large number of small, clumped chromosomes during metaphase I and II. Although it was estimated to have over 48-bivalent chromosomes, it may very well be $n = 60$; additional material is needed. This species is closely related to *C. pectinata* Matens & Galeotti, differing only in having leaves that are entire to 3-lobed rather than usually pinnately 5–7-lobed.

**Castilleja roei** Crosswhite

The count of $n = 12$ from four collections represents the first report for this species, although Holmgren (1976) indicated our unpublished count from the herbarium labels. *Castilleja roei* is undoubtedly related to *C. tenuifolia* in section *Epichroma* Benth. This is a beautiful species, easily recognizable by its habitat of dripping wet cliffs, perennial habit, filiform leaf segments, and especially its calyx coloration. Holmgren (1976) remarked that this is the only species of *Castilleja* in which the calyx is yellow distally and red proximally.

**Castilleja saltensis** Eastwood

The count of $n = 12$ from two populations collected in Durango agrees with one previously reported, also from Durango (Heckard, 1968). This species is perhaps related to *C. shaffneri* in such features as a dwarf, caespitose habit and a dense, compact floral spike, but is easily identified by its distally dilated, obtuse or rounded lobes of the floral bracts.

**Castilleja schaffneri** Hemsley

Chromosome counts of $n = 12$ were determined from three populations and are in agreement with one previously reported (Beaman et al., 1962). This species is easily distinguished by its dwarf, caespitose habit with many slender decumbent pilose stems from the base and dense spikes with large (mostly 3–4 cm long) red flowers and densely pilose calyx with shallowly cleft lateral lobes. It is distributed in the states of Hidalgo, México, Morelos, Puebla, and Veracruz, at elevations from 2,400 to about 4,000 m. It was meticulously illustrated by Hemsley (1882: 662, pl. LXII. B. figs. 7–13). Nesom (1992b) placed *C. schaffneri* and *C. pringlei* Fernald in synonymy with *C. moranensis* Kunth. However, this suggestion needs further investigation, especially careful study of the type specimen of *C. moranensis*. Eastwood (1909) treated these three species in sect. *Euchroma* (Nutt.) Benth.

**Castilleja scorzonerifolia** Kunth

The report of $n = 12$ from seven populations represents the first count for this species. *Castilleja scorzonerifolia* is a widely distributed species complex, ranging from northeastern to south-central Mexico. Nesom (1992b) reduced *C. lithospermoides* and *C. glandulosa* to synonymy under *C. scorzonerifolia* and pointed out, "It is somewhat variable in features of vestiture, calyx morphology, and degree of corolla exsertion, but for the most part, identifications of this species are relatively constant." The entire complex needs further study.

As indicated earlier, the discovery of at least four seed forms in this complex (including *C. lithospermoides* and *C. jiquilpana*) by our cursory investigation of specimens at hand suggests that detailed SEM study of seeds may help to unravel some of the taxonomic problems in this species group.

**Castilleja stenophylla** M. E. Jones

The chromosome count of $n = 12$ from six populations, all from Chihuahua, represents the first report for this species. This species is perhaps related to *C. integra*, but is distinguished by its entire linear leaves and smaller flowers. Eastwood (1909) placed it in sect. *Hemichroma* Benth., but we prefer to include it in sect. *Euchroma* (Nutt.) Benth. on account of its subequally cleft calyx, floral bracts that are broader than cauline leaves, and densely spicate inflorescence.

**Castilleja subinclusa** Greene
subsp. **subinclusa**

We have recently treated *C. subinclusa* as a highly variable species consisting of two subspecies, subsp. *subinclusa* (including *C. jepsonii*) and subsp. *franciscana*, distributed in cismontane California and northern Baja California (Chuang & Heckard, 1992b). This polyploid complex, one of many in the western United States, has four ploidy levels, $n = 12$ to 48, based on an exhaustive chromosome survey (Heckard, 1968; Chuang & Heckard, unpublished data). It is closely related to the wide-

ranging *C. linariifolia* Benth.; both species were included in sect. *Hemichroma* (= sect. *Castilleja*) by Bentham (1846). Pennell (1951) proposed section *Linariaefolia* to accommodate these two species because they share such features as an unevenly cleft calyx with a much deeper cut in front, and a corolla generally curved forward through a calyx sinus.

All three counts from northern Baja California are tetraploid ($n = 24$); the tetraploid populations of this species are also found randomly distributed north to the northern coastal counties of the San Francisco Bay area.

**Castilleja talamancensis** N. Holmgren

The count of $n = 12$ represents the first report for this species. This species, endemic to the Cordillera de Talamanca, Costa Rica, is similar to *C. irazuensis*.

**Castilleja tapeinoclada** Loesener

This count of $n = 12$ agrees with a previous report (Beaman et al., 1962) for this high-mountain (2,700–4,000 m) species, which is endemic to Guatemala. It is easily identified by its low (less than 10 cm high ) and spreading stature, and inflorescence with few (1–4), large flowers.

**Castilleja tenuiflora** Benth.

This, the most widely sampled species (17 populations) in our study, reveals two ploidy levels ($n = 12, 24$). This extensive survey does not show any specific cytogeographic distinctions between the diploid and tetraploid populations. The counts of $n = 12$ represent the first reported diploid, whereas the counts of $n = 24$ confirm a previous report (Heckard, 1968) for this most common, most widespread (extending from Guererro and Oaxaca, northward through most of Mexico to southeastern Arizona), and one of the most complex Mexican species. It is likely that some of the geographic variants such as a linear-leaved form, some color forms, and a form with a secund inflorescence and longer pedicels, represent populations intermediate between this and the closely related *C. integrifolia*, and perhaps even *C. tenuifolia*. Holmgren (1976) treated the following as conspecific with *C. tenuiflora*: *C. canescens* Benth., *C. laxa* A. Gray, *C. retrorsa* Standley, *C. xylorrhiza* Eastwood, *C. scabridula* Eastwood, and *C. setosa* Pennell.

**Castilleja tenuifolia** Marens & Galeotti

The count of $n = 10$ from five collections is actually the first report for this species, although Heckard (1968) pointed out an uncertain count of $n = 10$; that count was not reported in the list and no voucher specimen was cited. This species was included in the small sect. *Epichroma* by Bentham (1846). Eastwood (1909) stated, "*Epichroma* is probably the most individual subdivision and has, perhaps, the best claim to generic rank . . . ." The same number of $n = 10$ is found also in the closely related *C. gracilis* and distantly related *C. lineariloba* (subg. *Colacus* sect. *Onchorhynchus*). All the other *Castilleja* species counted have a chromosome number of $n = 12$ or multiples of the basic number; the number $n = 10$ is postulated to be an aneuploid reduction from an $n = 12$ progenitor.

The species is easily distinguishable by its annual habit, filiform leaf divisions, secund-racemose inflorescence, and funnelform and colorful calyces. It is distributed in Jalisco, Michoacán, México, Guererro, and Oaxaca.

**Castilleja virgata** (Wedd.) Edwin

This count of $n = 12$ represents the first report for this species. It is very similar to the highly variable *C. fissifolia*. The entire *C. fissifolia* complex is in urgent need of further critical study.

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# PHYLOGENETIC RELATIONSHIPS OF THE BROMELIIFLORAE–COMMELINIFLORAE–ZINGIBERIFLORAE COMPLEX OF MONOCOTS BASED ON *rbc*L SEQUENCE COMPARISONS[1]

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## Abstract

Four cladistic hypotheses were constructed for Dahlgren's Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex, primarily from suggestions of affinities according to morphology-based treatments: (i) Dahlgren's treatment of the families is correct; (ii) the Bromeliaceae and Zingiberales are sister groups; (iii) the complex is monophyletic, with the Arecaceae as the closest outgroup; and (iv) a clade that contains the Bromeliaceae and Commelinaceae is monophyletic. These four hypotheses were evaluated using sequence data from the chloroplast gene, *rbc*L, that codes for the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase. Results were compared between a broad analysis of 499 *rbc*L sequences and a smaller data set that included only families of the complex plus the Arecaceae (52 taxa). The larger data analysis supported hypothesis (iii), minus the Velloziaceae. However, hypotheses (i) and (ii) were not supported, and support for hypothesis (iv) was equivocal. Three decisions on classification can be made based on the results of this study: (i) submerge the Bromeliiflorae into the Commeliniflorae; (ii) remove the Velloziaceae from the complex; and (iii) remove the Cyclanthaceae and Pandanaceae from the Areciflorae.

Studies on the phylogeny and classification of the monocots (Liliopsida) have received considerable emphasis recently among plant systematists. One of the major difficulties, however, has been the relative dearth of morphological characters (compared with the dicots) that are consistently useful for phylogenetic inference. This is probably due both to a general uniformity in floral morphology of monocots (the trimerous "Lilioid" flower) and the occurrence of extremely reduced or specialized floral structures that obscure evolutionary relationships of several key groups. Accordingly, major classifications show significant differences in the treatments of monocots (Cronquist, 1988; Dahlgren et al., 1985; Takhtajan, 1980; Thorne, 1992).

The group of focus in this study is a three-superorder complex, as outlined by Dahlgren et al. (1985), that includes the Bromeliiflorae (six orders), the Commeliniflorae (four orders), and the Zingiberiflorae (one order). Within this group, the family of interest for this project is the Bromeliaceae, a well-defined family that is widely recognized as monophyletic based on several synapomorphies (Gilmartin & Brown, 1987). However, its relationships to other families and its taxonomic position within the monocots are in dispute. Therefore, we constructed four cladistic hypotheses to

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explain the relationships of the Bromeliaceae and related monocots, as follows: (i) Dahlgren's treatment (Dahlgren & Bremer, 1985) of the families, modified with more recent data (Gilmartin & Brown, 1987; Simpson, 1987, 1990), is correct (Fig. 1); (ii) the Bromeliaceae and Zingiberales are sister groups (Fig. 2); (iii) the complex is monophyletic, with the Arecaceae as the closest outgroup (Fig. 3); and (iv) a clade that contains the Bromeliaceae, Commelinaceae, and other commelinoids is monophyletic (Fig. 4). These hypotheses were evaluated by comparison with results from parsimony analyses of DNA sequences from the chloroplast gene *rbc*L.

## Classification

Traditional classifications of plants have necessarily served as the starting point for defining the scope of taxa to be used in modern phylogenetic analyses. However, past and current classifications of some families, such as the Bromeliaceae, are so diverse as to render this process difficult. Major taxonomic treatments put the Bromeliaceae in a variety of higher categories. Takhtajan (1980) considered the Bromeliaceae to be a member of his superorder Lilianae. Other authors have included the commelinoid monocots with the bromeliads (Hutchinson, 1973; Thorne, 1992). However, Cronquist (1978) found the Bromeliaceae to be highly discordant in the subclass Commelinidae; he instead placed them in his Zingiberidae, along with the Zingiberales (formerly in the Liliidae). This change was prompted, at least in part, by a desire to sharpen the definition of the Commelinidae and the Liliidae. Finally, the most divergent view of bromeliad classification among major treatments may be that of Dahlgren et al. (1985), who placed the Bromeliaceae in the superorder Bromeliiflorae, along with four other single-family orders and the two-family order Typhales.

## Phylogenetic Relationships

Identification of shared derived character states using phylogenetic systematics provides a rigorous methodology for inferring evolutionary relationships and for evaluating previous notions of classification. However, many character states that have been used to define taxa are unknown with respect to polarity and may represent primitive retentions. For example, Cronquist (1978) suggested a relationship between Bromeliales and Zingiberales based on their large, showy bracts. Williams & Harborne (1977) made the same suggestion based on the myricetin and quercetin glycosides that occur in both groups. Takhtajan (1980) proposed a relationship between bromeliads and lilialean families, especially Agavaceae, based on numerous similarities: raphides, steroidal sapogenins, flavonoids, scalariform perforations in root vessels, septal nectaries, helobial endosperm, and ". . . definite similarities between pollen grains" (p. 314). The literature is replete with such suggestions. Nonetheless, these suggestions do not tell us which characters are indicators of common ancestry (synapomorphic). The most thorough and perhaps strongest suggestions for the phylogenetic relationships of the bromeliads come from the work of Dahlgren and his associates (Dahlgren & Rasmussen, 1983; Dahlgren & Bremer, 1985; Dahlgren et al., 1985). Although their character polarities were offered as provisional, the monophyly of the Bromeliaceae is apparently supported by three consistent synapomorphies. These are: (i) stellate and scalelike multicellular hairs; (ii) large, solitary silica bodies; and (iii) a conspicuously sepaloid and petaloid perianth. However, only the stellate or scalelike multicellular hairs are unique to the Bromeliaceae; other traits are homoplastic. Additional synapomorphies for the Bromeliaceae might include conduplicate-spiral stigmas (Brown & Gilmartin, 1989a) and a base chromosome number of $x = 25$ (Brown & Gilmartin, 1989b). But the consistency of these characters across the family awaits a more complete evaluation.

The greatest number of ideas about the phylogenetic relationships of the Bromeliaceae involve interfamilial and interordinal levels because these present the greatest difficulty. Cronquist (1988) suggested that the Bromeliales shared a common ancestor with the Zingiberales that ". . . might have been much like some of the more archaic, terrestrial Bromeliaceae, but less xerophytic" (p. 487). The monocot "phylogeny" of Walker (1986) shows the Bromeliidae and the Commelinidae arising together from the Liliidae. Dahlgren & Rasmussen (1983) included the Bromeliaceae with the Velloziaceae, Philydraceae, Haemodoraceae, Pontederiaceae, Typhaceae, and Sparganiaceae in the superorder Bromeliiflorae. However, the sister status of the Bromeliaceae in Dahlgren's system is shown as a polytomy that consists of the bromeliads, the Velloziales, and collectively all of the remaining orders of the Bromeliiflorae.

Sister status of Bromeliaceae and Velloziaceae was more firmly suggested in a cladistic study by Gilmartin & Brown (1987). This suggestion was derived from sequential analyses of likely sister groups, a methodology that was criticized by Simpson (1988) but defended by Gilmartin & Brown

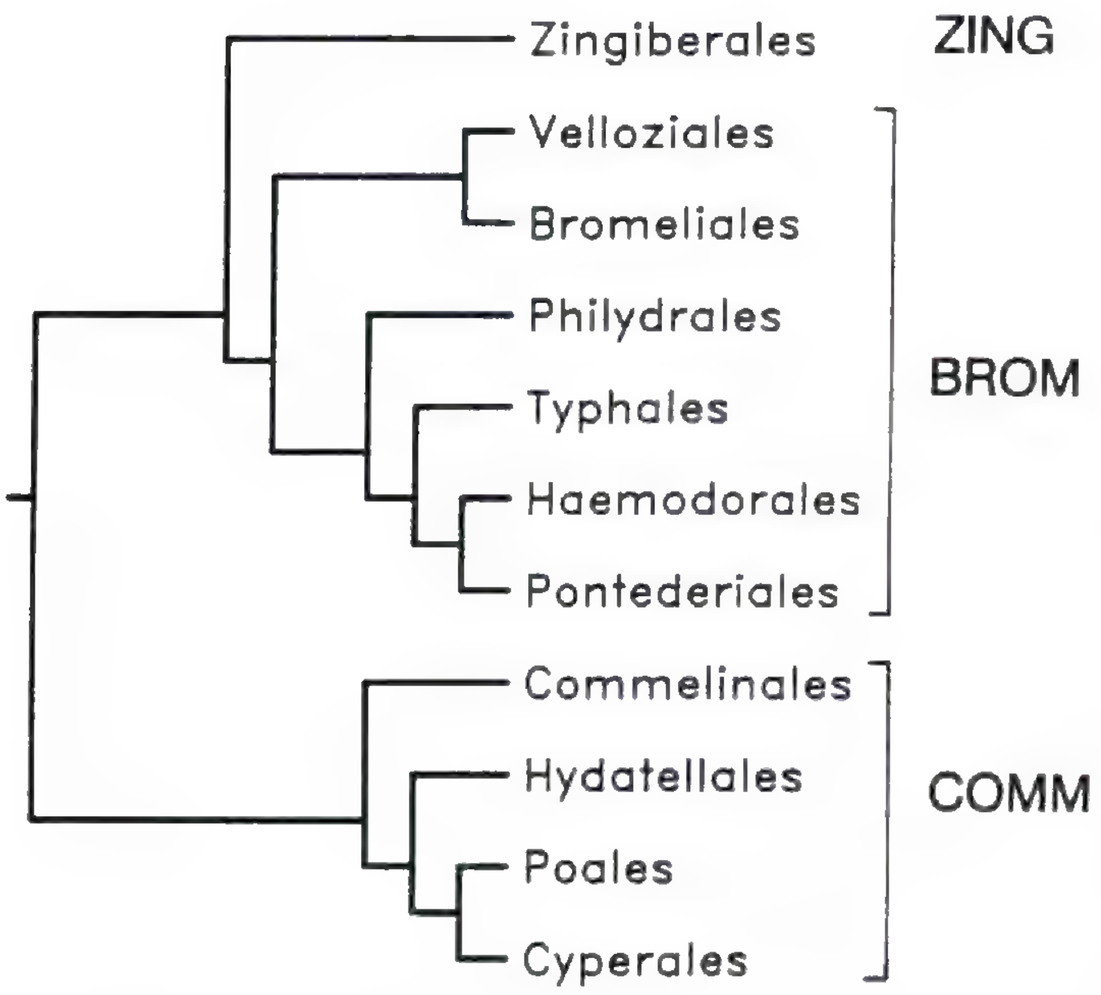


FIGURE 1. Hypothesis 1: Relationships within the three- superorder complex. ZING = Zingiberiflorae, BROM = Bromeliiflorae, COMM = Commeliniflorae.

(1988). Regardless, no synapomorphies were identified that distinguished a Bromeliaceae–Velloziaceae clade from the other families examined.

At a more inclusive taxonomic level, monophyly of the Bromeliiflorae is supported in the Dahlgren scheme by an apomorphic subtype of helobial endosperm. Furthermore, this scheme shows that the sister group to the Bromeliiflorae is the Zingiberiflorae (demonstrated by showy perianths). The Commeliniflorae are sister to the Bromeliiflorae–Zingiberiflorae clade. The monophyly of this three-superorder complex is supported by three synapomorphies: sculptured and oriented epicuticular wax ("*Strelitzia*-type"), endosperm with copious starch, and cell walls with UV-fluorescent compounds.

## OBJECTIVES AND HYPOTHESES

Given the variety of classifications and suggested phylogenetic relationships for the Bromeliiflorae–Commeliniflorae–Zingiberiflorae, our main objective was to obtain new information regarding the relationships among the constituent families in these groups. This new information consists of a cladistic analysis of nucleotide sequences of the plastid gene *rbc*L, which codes for the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase.

We have constructed four hypotheses for evaluation by DNA sequence comparisons. We chose Dahlgren's system as a framework for our initial hypothesis. Although there have been many suggestions about the possible relationships of the complex, those of Dahlgren and his associates are the most comprehensive and the closest to being explicit cladistic hypotheses (Dahlgren & Bremer, 1985). However, we have modified the polytomy (Velloziales, Bromeliales, all other Bromeliiflorae) in Dahlgren's Bromeliiflorae to reflect the study by Gilmartin & Brown (1987). This change shows the Bromeliaceae and Velloziaceae to be sister taxa. We have also modified the polytomy (Haemodorales, Pontederiales, Typhales) to reflect relationships suggested by Simpson (1987, 1990). This change shows the Haemodoraceae/Haemodorales and Pontederiaceae/Pontederiales to be sister taxa. Accordingly, our initial hypothesis for the phylogenetic relationships of the three superorder complex is summarized in Figure 1.

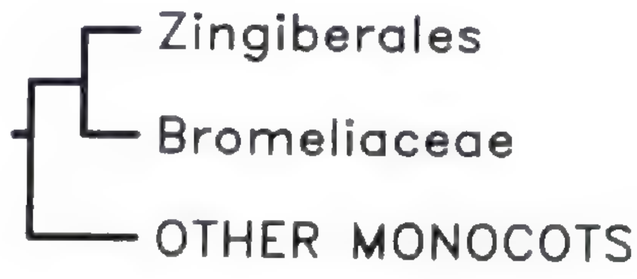


FIGURE 2. Hypothesis 2: Closest outgroup status of the Bromeliaceae to the Zingiberales.

Our second hypothesis is that the Bromeliaceae and Zingiberales are sister taxa (Fig. 2). This explanation is based in part on suggestions of Cronquist (1988) regarding the putative common ancestor to the two groups. It also incorporates the observation of Kress (1990) that, at present, the Bromeliaceae are the best outgroup to the Zingiberales.

Our third hypothesis is that the Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex is a monophyletic group, as suggested by Dahlgren & Rasmussen (1983). This group is held together by the three synapomorphies mentioned previously. However, at the moment, there is no clear guidance for suggesting a putative sister group to this complex. Thus, this hypothesis is the most incomplete of the four examined in this study. Nevertheless, a tentative proposal might include the Arecales, whose members also possess UV-fluorescent cell walls (Fig. 3).

Our fourth hypothesis is that the Bromeliaceae and Commelinaceae are together in a "commelinoid–bromelioid" clade (Fig. 4), which precludes the Bromeliaceae–Zingiberales proposed in the second hypothesis (Fig. 2). The fourth hypothesis derives from the inclusion of bromeliads within the Commelinales by Thorne (1992), from the putative derivation of the Bromeliales from the Commelinales proposed by Hutchinson (1973), and from the common origin of the Bromeliidae and Commelinidae suggested by Walker (1986). However, this alternative hypothesis cannot be developed enough at the moment to predict with certainty which

FIGURE 3. Hypothesis 3: Monophyly of the three-superorder complex and closest outgroup status of the Arecaceae to the complex. Synapomorphies marked on the cladogram are: 1, UV-fluorescent cell walls; 2, copious endosperm; 3, *Strelitzia*-type epicuticular wax.

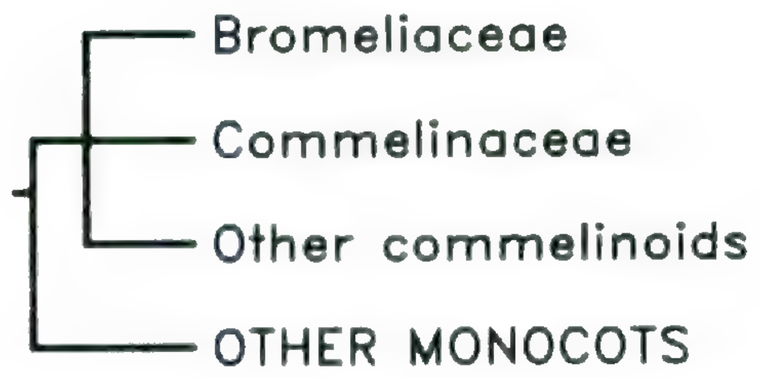


FIGURE 4. Hypothesis 4: Monophyly of a group containing the Bromeliaceae and Commelinaceae.

monocots, outside of the Bromeliaceae and Commelinaceae, should be considered as commelinoid.

There are undoubtedly other nontrivial hypotheses that we could have examined for this paper. However, focus on this particular set of hypotheses was guided by numerous preliminary analyses as the project grew. For this reason, our method is not only abductive and predictive but also in part retrodictive. The method is retrodictive because we chose our hypotheses after we examined preliminary results. Nevertheless, we believe that this mixed process has enabled us to make significant progress in monocot systematics.

Our hypotheses are not completely mutually exclusive, but neither can all be fully supported. This means that our results should be useful for evaluating morphological and chemical character evolution on *rbc*L-based trees. Accordingly, we can make preliminary character analyses of those traits that have traditionally been used for suggesting phylogenetic relationships.

## MATERIALS AND METHODS

Sequences were obtained from seven genera of the Bromeliaceae and one genus each from the Strelitziaceae, Pontederiaceae, Velloziaceae, and Rapateaceae. Other sequences used for comparison here either have been published or shared by other investigators. Sources for new sequences used in this report are listed in the Appendix.

In most instances total DNA was extracted from fresh leaf tissue using a Tris-EDTA buffer (Dellaporta et al., 1983). In contrast, samples of *Stegolepis*, *Vellozia*, and *Glomeropitcairnia* were extracted using the CTAB microextraction method of Learn (1987). Each preparation was used to provide a template for amplifying *rbc*L by the polymerase chain reaction (PCR). The PCR protocol was suggested by the supplier of *Taq* DNA polymerase (Promega Corp.). Primers for amplifying double-stranded DNA were designed from conserved regions in *atp*B from *Nicotiana tabacum*, in *rbc*L from *Zea mays*, and in ORF106 from *Oryza sativa* (Golenberg et al., 1990). Single-stranded DNA was made in a second round of PCR using the double-stranded product as a template. Single-stranded products were cleaned by precipitation in NaOAc. Both the coding strand and the complementary strand were amplified separately and subsequently sequenced. Sequencing followed Sanger et al. (1977) according to the Sequenase protocol (US Biochemical). Internal sequencing primers were provided by G. Zurawski (DNAX Corp., Palo Alto, California) from conserved regions in the *rbc*L sequence of *Zea mays*.

Sequence data were read directly from autoradiograms into files created by a sequence editor (SE; Matt Clegg, Riverside, California). Sequences were aligned by hand. Ultimately, all sequences were entered into an edit file in the NEXUS format for parsimony analysis with PAUP 3.0 (Swofford, 1991).

For this paper, a subset of genera was reanalyzed separately from the 499 taxa of seed plants used by Chase et al. (1993). This subset included 52 species of monocots from 20 families in the Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex, plus the Arecaceae (Table 1). We deemed the analysis of this subset useful because of its potential for evaluating in more detail a smaller set of ingroup relationships. Fitch parsimony analyses (equal weighting) were performed on 10 random-addition data sets of the 52 taxa. Character-state changes were plotted using the ACCTRAN option. The most parsimonious trees from these analyses were also used as the starting point for a character-state weighted analysis of the 52 taxa (Albert et al., 1993).

## RESULTS

Figure 5 shows the relationships between the ingroup (i.e., the Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex) for this study and other families of monocots. This cladogram was made by modifying Figures 5A and 6A from the 499-taxon analysis in Chase et al. (1993) to include only

family names and exclude names of genera. This simplification is justified because all of the families for which multiple genera were sampled are monophyletic in this cladogram, with the exception of the Melianthaceae.

Figure 5 shows not only the position of the ingroup relative to other monocots, but also the exclusion of the Velloziaceae from the ingroup. A sister-taxon relationship between the Velloziaceae and Bromeliaceae is clearly not supported by *rbc*L sequence data. The Velloziaceae are instead far removed from the three-superorder complex of interest here, to sister status with a Pandanaceae–Cyclanthaceae clade. This result provides support for Cronquist's inclusion of the Velloziaceae in the Liliales, but an explicit hypothesis for this relationship is beyond the scope of this paper. Nevertheless, this finding provides direction for future studies on the relationships of the Velloziaceae.

Figure 6 is modified from Chase et al.'s (1993) 499-taxon analysis to show relationships among the ingroup families for this study. Most multiple-sample families are again monophyletic, the exceptions being the Juncaceae and Cyperaceae. Figure 6 shows Dahlgren's Bromeliiflorae and Commeliniflorae to be paraphyletic. The only family from Dahlgren's Bromeliiflorae that diverges with the bromeliads is the Typhaceae. All of the other families in this clade are members of Dahlgren's Commeliniflorae. In addition, the bromeliad-containing clade shows the Bromeliaceae to be basal within it. This implies that there is no single sister family to the Bromeliaceae.

The remaining bromeliiflorean families in Figure 6, plus the Commelinaceae, diverge with the Zingiberales. Regardless of the lack of support for Dahlgren's concept of the Bromeliiflorae and Commeliniflorae, these results do support the monophyly of the Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex (minus the Velloziaceae). Furthermore, the Arecaceae appear as the outgroup to this three-superorder complex, as also suggested in Figure 5.

Reanalysis (unrooted) to include just the Arecaceae and the ingroup of interest yielded 198 most-parsimonious trees of length 1665 by Fitch parsimony. A strict consensus showed that differences among trees were due to within-family rearrangements in the Bromeliaceae and Poaceae (data not shown), so all family-level nodes were fully resolved (Fig. 7A). Character-state weighting yielded 30 most parsimonious trees, each of which converted to 1667 even-weighted steps. A strict consensus showed that differences among trees were again due to within-family rearrangements, so all family-level nodes were still fully resolved. However, there was one family-level difference between the Fitch analysis and the weighted analysis: the Commelinaceae moved from a position basal to the Pontederiaceae–Philydraceae–Haemodoraceae clade (Fig. 7A) to a position that is sister to the Pontederiaceae (Fig. 7B).

TABLE 1. Families analyzed in this study. (The first number in parentheses is the number of species examined; the second number is the approximate minimum number of species in the family according to Thorne, 1992.)

| | |
|---|---|
| Arecaceae (7/2780) | Marantaceae (2/500) |
| Bromeliaceae (7/1520) | Musaceae (1/42) |
| Commelinaceae (3/605) | Philydraceae (1/6) |
| Costaceae (2/150) | Poaceae (9/10,000) |
| Cyperaceae (2/5315) | Pontederiaceae (1/30) |
| Flagellariaceae (1/4) | Rapateaceae (1/80) |
| Haemodoraceae (1/80) | Restionaceae (1/407) |
| Heliconiaceae (1/250) | Strelitziaceae (3/7) |
| Juncaceae (3/300) | Typhaceae (1/30) |
| Lowiaceae (1/6) | Zingiberaceae (4/1000) |

Several changes occurred among family relationships by analyzing the smaller data set. Perhaps the most notable of these is that the four-family clade containing the Commelinaceae shifted from the Zingiberales-containing clade to a more conventional position near the Cyperales and other commelinoid monocots (Fig. 7A). In so doing, the Commelinaceae-containing clade replaced the Flagellariaceae as a sister group to the Cyperales. The Flagellariaceae, in turn, moved to a position basal to the Restionaceae–Poaceae family pair. An internal rearrangement in the Commelinaceae-containing clade also put the Haemodoraceae and Philydraceae together as sister taxa, which roughly conforms to the recent cladistic analysis by Simpson (1990). The difference is that our results show the Philydraceae and not the Pontederiaceae as the sister group to the Haemodoraceae. The Pontederiaceae are instead basal to the Philydraceae–Haemodoraceae clade.

Finally, results from this analysis also show a sister family relationship between the Bromeliaceae and the Rapateaceae. The Bromeliaceae–Rapateaceae clade is sister to a clade containing all the remaining families of the Bromeliiflorae and Commeliniflorae in the ingroup.

## DISCUSSION

The results reported here provide little support for Dahlgren's view of the Bromeliiflorae. Moreover, there is no evidence from *rbc*L sequence comparisons that the Velloziaceae are the sister

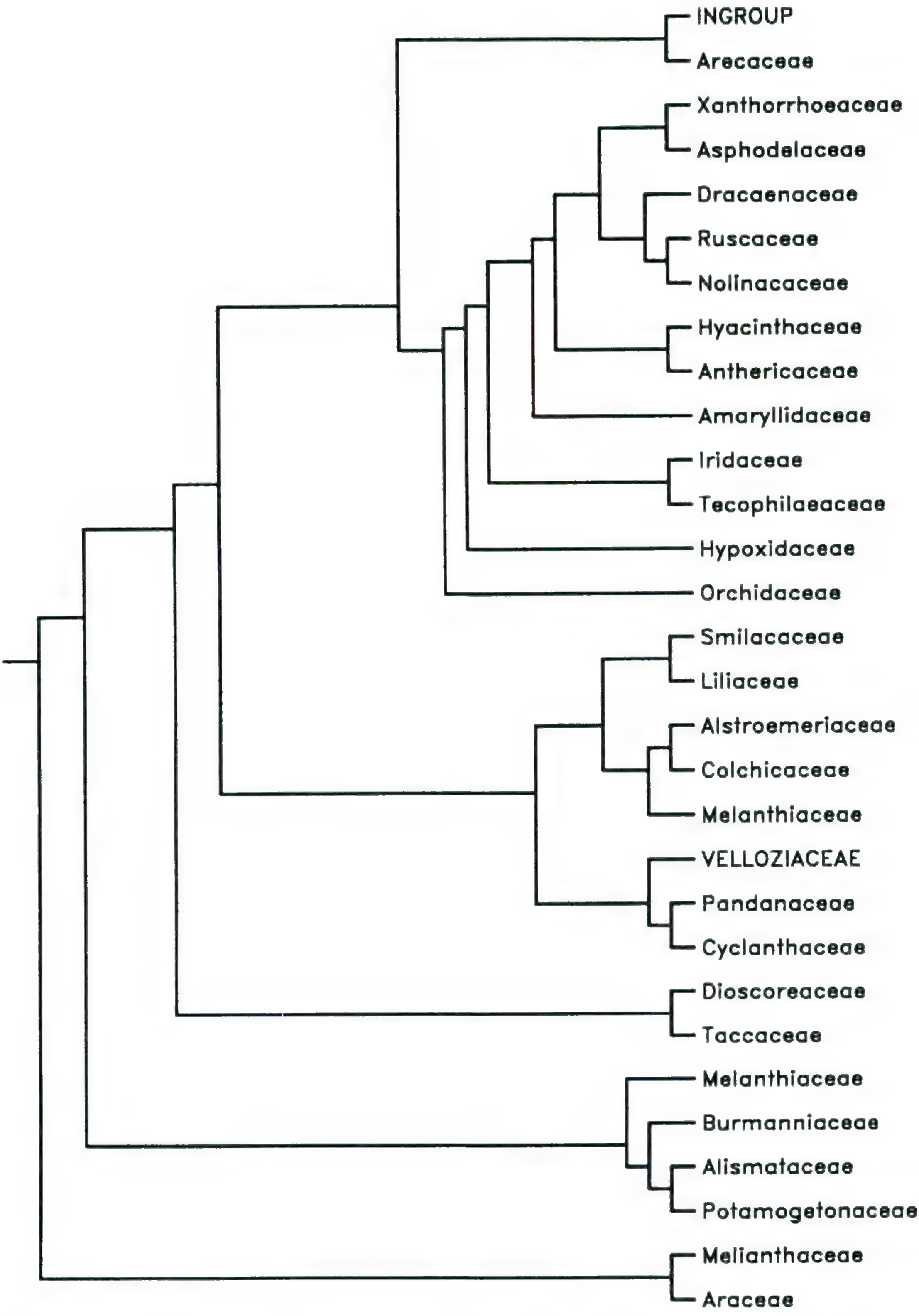


FIGURE 5. Relationships of the INGROUP/Arecaceae clade to other monocot groups according to unrooted parsimony analysis of a 499-taxon data set of seed plants. INGROUP = Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex, minus the Velloziaceae. Modified from Chase et al. (1993).

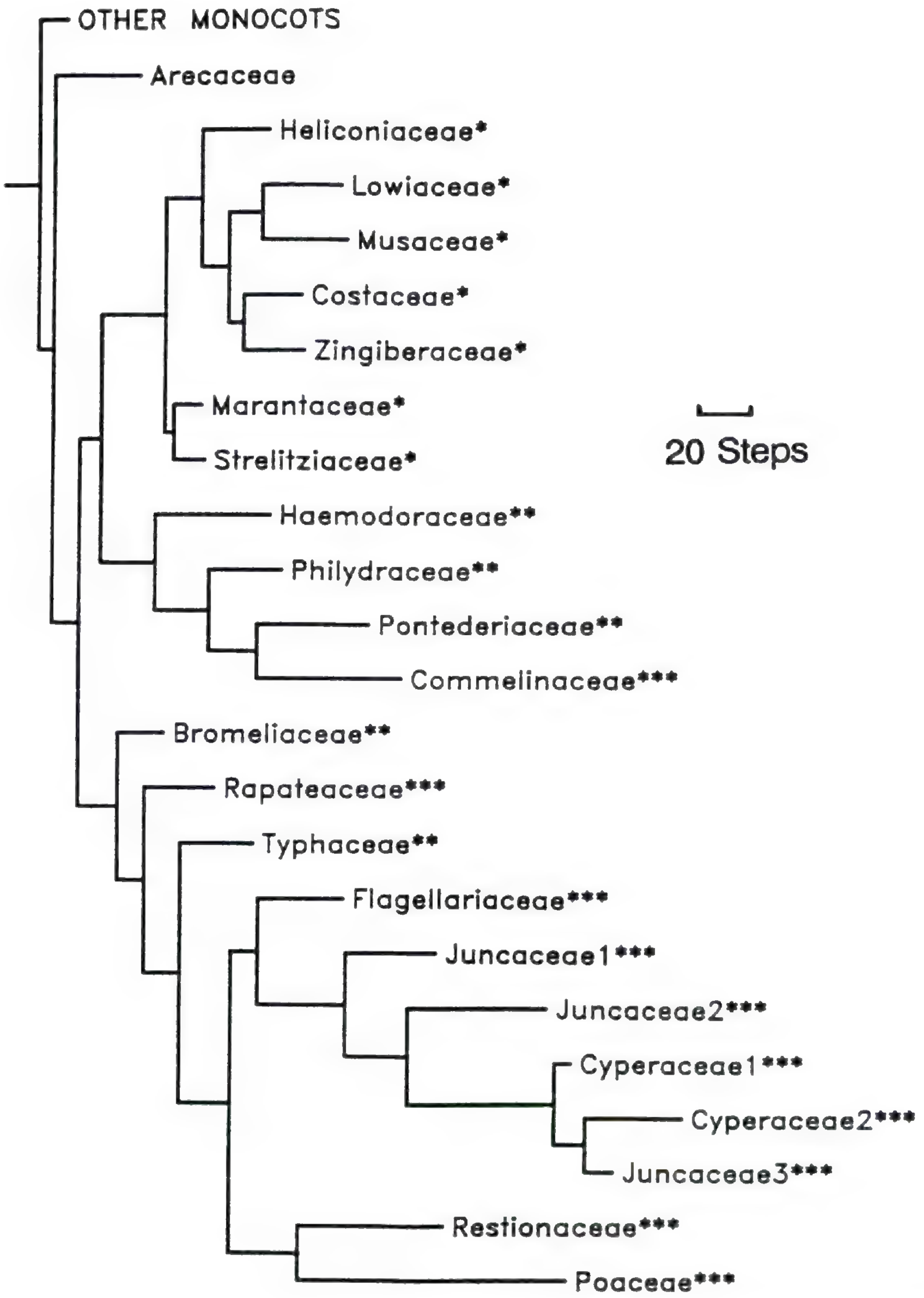


FIGURE 6. Family-level relationships within the Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex according to unrooted parsimony analysis of a 499-taxon data set of seed plants. Modified from Chase et al. (1993). * = Zingiberiflorae; ** = Bromeliiflorae; *** = Commeliniflorae.

family to the Bromeliaceae. Therefore, we reject our first hypothesis. The rejection of Dahlgren's Bromeliiflorae comes as no surprise, since this superorder is held together by a single provisional synapomorphy, a variant form of helobial endosperm. In general, helobial endosperm is characterized by a division of the primary endosperm nucleus, which is followed by the formation of a transverse cell wall. This cell division makes a larger micropylar chamber and a smaller chalazal chamber (Dahlgren & Clifford, 1982). However, all but the Pontederiaceae of Dahlgren's Bromeliiflorae are known to have a much smaller, starch-free chalazal chamber. Dahlgren & Rasmussen (1983) suggested that the Pontederiaceae probably have this subtype of helobial endosperm. In addition, this character is homoplastic because a very small, starch-free chalazal chamber also occurs in the helobial endosperm of *Thismia javanica* of the Burmanniaceae (Dahlgren & Clifford, 1982), a

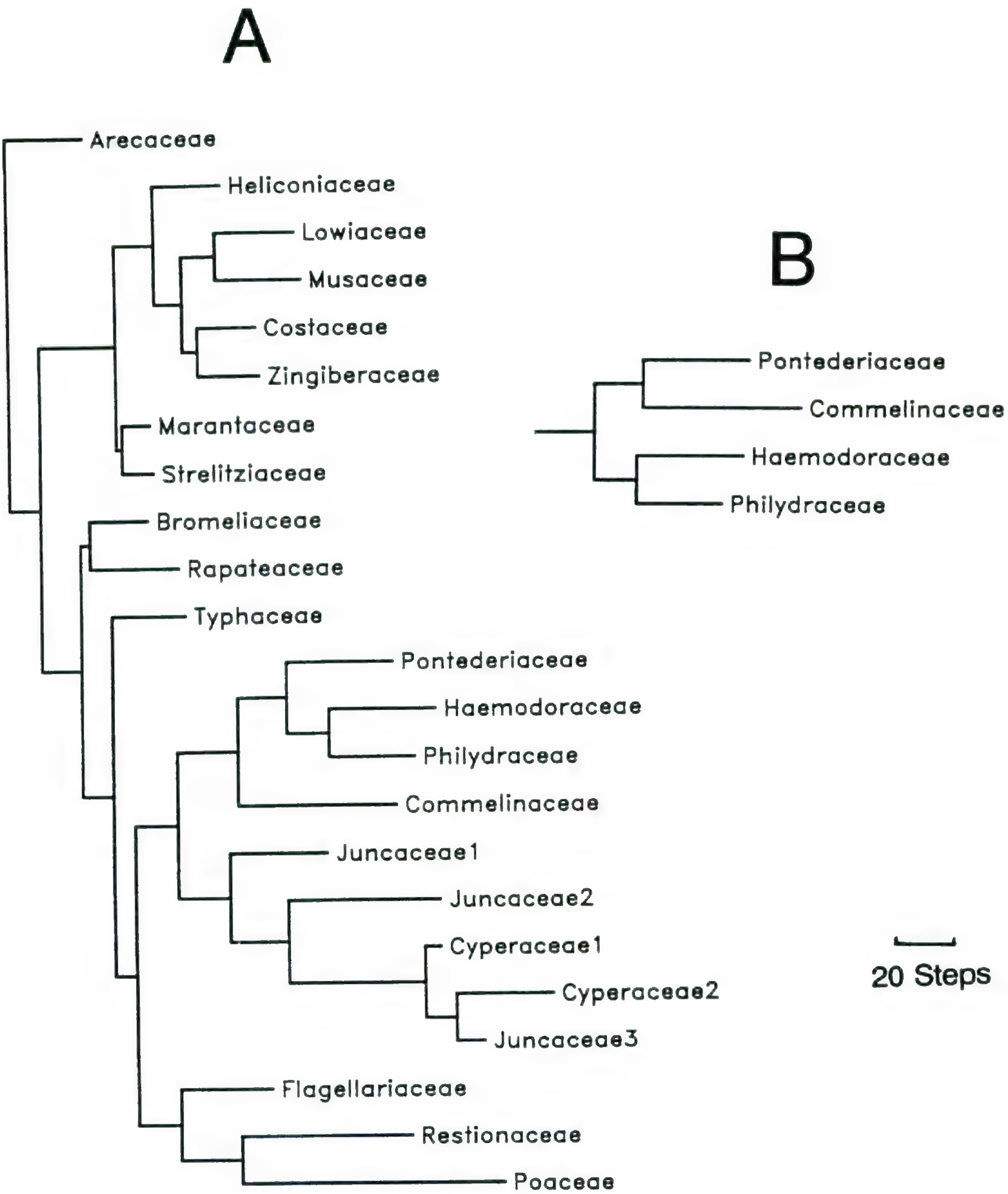


FIGURE 7. Family-level relationships within the Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex according to unrooted parsimony analyses of a 52-taxon data set of monocots. (A) Strict consensus of 198 trees generated by Fitch analysis (equal-weighting); length = 1665. (B) Family-level rearrangement generated by character-state weighted parsimony analysis, strict consensus of 30 trees; length = 1667. Changes among trees in both analyses occurred only within families (not shown).

family that is not believed to have a close relationship with the Bromeliiflorae (Dahlgren & Bremer, 1985).

The occurrence of biflavonoids in *Xerophyta plicata* (Velloziaceae) and their absence in the Bromeliaceae lends no support to a close relationship between the Bromeliaceae and the Velloziaceae. Biflavonoids are extremely rare in monocots, so their occurrence in the Velloziaceae may be autapomorphic. If biflavonoids are of phylogenetic sig-

nificance among monocot families, then hypotheses regarding the relationship of the Velloziaceae, Cyclanthaceae, and Pandanaceae should be examined. The latter two families are the closest to the Velloziaceae according to analysis of *rbc*L sequences (Chase et al., 1993; Duvall et al., 1993).

We also reject our second hypothesis, that the Zingiberales and Bromeliaceae form a monophyletic lineage. This means that the conventional characters shared by these groups (large, showy bracts and petaloid perianth parts) do not support a unique relationship; these character states are better interpreted as plesiomorphies. Other groups also have showy bracts (Orchidaceae and some Araceae, among others) or petaloid perianth parts (Commelinales and nearly all of Dahlgren's Liliiflorae). Such a diverse distribution suggests that these characters are either nonhomologous (Kress, 1990), homoplastic, or symplesiomorphic. Regardless, they do not appear to be synapomorphic for the Bromeliaceae and Zingiberales. Furthermore, initial evidence for a common ancestry based on flavonoid chemistry (Williams & Harborne, 1977) was quickly refuted following a more detailed examination of the Bromeliaceae (Williams, 1978). Thus, our results show that the Zingiberidae of Cronquist are paraphyletic, and the traditional chemical and morphological characters that support their monophyly are equivocal or unlikely to be informative.

Monophyly of the Bromeliiflorae–Commeliniflorae–Zingiberiflorae complex is supported by Chase et al.'s (1993) 499-taxon analysis (Fig. 6). Furthermore, the Arecaceae are the sister group to this triumvirate. This result supports our third hypothesis regarding the common ancestry of these three superorders. Therefore, we accept the hypothesis and agree with Dahlgren's view of this relationship, even though we reject his proposed ingroup phylogeny (first hypothesis). We also accept our tentative proposal to designate the Arecaceae/Arecales as the sister group to the three-superorder complex. Such designation clarifies the speculation by Dahlgren & Bremer (1985) that the Arecales are somehow related to the Commelinales. Their suggestion was speculative because they showed no synapomorphies to support it. On the other hand, similar speculation that the Pandanales and Cyclanthales might belong to Bromeliiflorae or Commeliniflorae, respectively, is not supported by *rbc*L comparisons (see Chase et al., 1993, fig. 5A).

By supporting our third hypothesis, we also make sense of the phylogenetic distribution of three apomorphies. These are a sculptured and oriented epicuticular wax ("*Strelitzia*-type"), an endosperm with copious starch, and UV-fluorescent cell walls (Fig. 3). The significance of these synapomorphies comes from their occurrence in the Arecales as well as in the ingroup. We therefore have strong, independent support for an Arecales-ingroup relationship. It is notable that the three characters in question are informative at a high taxonomic level. There are few other examples of such extensive support for higher categories. However, the distribution of these apomorphies does not preclude a Poales–Arecales relationship, as suggested by Dahlgren & Bremer (1985). But our *rbc*L analysis provides no support for such a relationship.

The main problems with the above synapomorphies lie in incompleteness of sampling and in inconsistency of distribution, which are perhaps expected consequences of circumscribing such a large group. For example, most Zingiberales have starchy perisperm or chalazasperm instead of starchy endosperm. Starchy endosperm may also be a synapomorphy for the Arales (Dahlgren & Rasmussen, 1983), thereby making this character homoplastic within the monocots. Moreover, the significance of starchy endosperm in the unripe seeds of some Burmanniaceae is unclear. All starch in these seeds is exhausted by the time they ripen. Thus, homology is uncertain for this character.

Similarly, *Strelitzia*-type epicuticular wax is common only in the Arecaceae, Cannaceae, Cyperaceae, Heliconiaceae, Juncaceae, Poaceae, Strelitziaceae, and Typhaceae and rare in the Bromeliaceae, as well as Velloziaceae (Behnke & Barthlott, 1983). In addition, smooth or nonoriented wax crystals often occur in the Poaceae, Cyperaceae, Marantaceae, Rapateaceae, Restionaceae, Xyridaceae, and Haemodoraceae. Wax crystals are absent from some Bromeliaceae, Haemodoraceae, Rapateaceae, Marantaceae, and Velloziaceae and from all taxa that were examined in the Zingiberaceae, Pontederiaceae, and Joinvilleaceae (Barthlott & Frölich, 1983).

Upon first inspection, the problem of inconsistency also seems to plague the distribution of UV-fluorescent cell walls within the monocots. For example, certain taxa in the Haemodoraceae do not have UV-fluorescent cell walls (Harris & Hartley, 1980). However, these taxa are more appropriately included in the Tecophilaeaceae, a family that is not closely related to the Haemodoraceae (Simpson, 1985, 1990). Fluorescent cell walls also occur in the Cyclanthaceae and the Xanthorrhoeaceae, which seems to indicate homoplasy for this character. However, the cell walls of these two families are fluorescent because of *p*-coumaric acid. Cell

wall fluorescence in other monocots is due to a combination of *p*-coumaric acid, ferulic acid, and diferulic acid. The latter combination is found only in the Arecales, the Bromeliiflorae, the Commeliniflorae and the Zingiberiflorae. Therefore, UV-fluorescence by ferulic acid and its dimer is a unique synapomorphy. (One minor exception may be the absence of diferulic acid in the cell walls of *Restio oligocephalus* [Restionaceae] (Harris & Hartley, 1980); we suspect that this compound will yet be found in this and other species of the family.) It is also notable that, among the taxa of interest here, only the Hydatellaceae, Costaceae and Heliconiaceae have not been examined for cell-wall ferulates.

Aside from the monocots, cell-wall ferulate is apparently synapomorphic for the Caryophyllales (Hartley & Harris, 1981) and perhaps for the Coniferophyta (Strack et al., 1988). In these groups, ferulic acid itself is the consistent character, whereas the distributions of *p*-coumaric acid and diferulic acid are more variable. In addition, the phylogenetic relevance of ferulic acid for the Coniferophyta is not known because no other nonflowering seed plants have been examined.

Ferulic acid is a relatively simple and probably common constituent of plants (Molgaard & Ravn, 1988), but it dimerizes and links cell-wall components only in certain plants of close affinity within the monocots, the dicots and perhaps the conifers. Because of their unique linkage to cell walls, these compounds constitute a potentially rich source of biochemical data for phylogenetic study. Specifically, a molecular systematic approach to the ferulate-cell wall pathway should yield strong evidence on the homology or nonhomology of this pathway in monocots and dicots. Such evidence would be important for evaluating the potential role of this pathway in the evolutionary origin of lignification (Fry, 1983; Kubitzki, 1987).

When all 499 genera of seed plants are analyzed (Chase et al., 1993), the Bromeliaceae and Commelinaceae are not in the same clade as predicted by our fourth hypothesis. This analysis instead shows the clade (Haemodoraceae, (Philydraceae, (Commelinaceae, Pontederiaceae))) to be the sister group of the Zingiberales; the Bromeliaceae are shown to be basal to another lineage. Support for the sister status of the Commelinaceae-containing clade and the Zingiberales comes from one potential synapomorphy: root hair cells that are shorter than other epidermal cells. This character state is not shared, however, with the Philydraceae and Pontederiaceae (Dahlgren & Bremer, 1985). On the other hand, there is no known support from morphology for distinguishing a Bromeliaceae-containing clade from a Commelinaceae-containing clade.

In contrast to the broad 499-taxon analysis of Chase et al. (1993), evaluation of a smaller *rbc*L data set (52 taxa) that included only the ingroup plus the Arecaceae did support our fourth hypothesis that the Bromeliaceae and Commelinaceae are part of the monophyletic group (Fig. 7A). However, there are no synapomorphies from morphology to corroborate this result at this time. The smaller analysis also showed a sister-taxon relationship between the Bromeliaceae and Rapateaceae (Fig. 6). These families were not sister taxa in the broad analysis, but the Bromeliaceae were shown to be basal to a clade that includes the Rapateaceae as its basal member.

## Conclusions

Analysis of *rbc*L sequences supports Dahlgren's concept of a clade consisting of his Bromeliiflorae, Commeliniflorae, and Zingiberiflorae. Furthermore, analysis of a 499-taxon data set showed the Areciflorae (Arecales only) to be basal to this complex (Chase et al., 1993). However, Dahlgren's concept of the Bromeliiflorae is no longer tenable. Most of the families and orders in this superorder show a complex pattern of affinities with his Commeliniflorae and Zingiberiflorae. The Velloziaceae are removed from the complex entirely. The Bromeliaceae are not the sister to the order Zingiberales. Instead, the Bromeliaceae are better placed at or near the base of the clade that is next to the zingiberalean lineage.

Three straightforward decisions on classification can be made based on our conclusions. One is to remove the Cyclanthaceae and Pandanaceae from the Areciflorae. The Areciflorae are thereby comprised of one family, the Arecaceae. The second decision is to remove the Velloziaceae from the ingroup of this study (i.e., the Bromeliiflorae, Commeliniflorae, Zingiberiflorae clade). Both of these decisions are in agreement with the broader molecular analysis of monocots presented by Duvall et al. (1993) and are supported by the synapomorphic distribution of UV-fluorescent cell walls in the Areciflorae and in the ingroup.

The third decision is to submerge the Bromeliiflorae into Dahlgren's Commeliniflorae. However, at this time there are no objective criteria for determining whether the Commeliniflorae are paraphyletic (Fig. 6) or monophyletic (Fig. 7A). The Arecaceae-ingroup portion of the tree in Figure 6, which supports the former, is 1663 steps, whereas the latter is indicated by the 1665-step tree in

Figure 7A. The choice between these two possibilities must await further study.

Many family-level topologies are not firm enough to warrant conclusions at this time. However, the topologies shown here should be used as hypotheses for further study. Additional work should include analyses of molecular data from more genera of the larger families that are included here (e.g., Cyperaceae, Juncaceae, Commelinaceae, Haemodoraceae, Zingiberaceae, Costaceae, and Marantaceae) as well as from families that were not included in this study: Cannaceae, Centrolepidaceae, Eriocaulaceae, Hydatellaceae, Mayacaceae, Sparganiaceae, Thurniaceae, Xyridaceae, and Joinvilleaceae. Family-level topologies should be examined among gene trees of genes that are less conservative than *rbc*L. Most importantly, future studies should include cladistic evaluations of morphological and chemical data. Preliminary data from UV-fluorescent cell walls, helobial endosperm, and *Strelitzia*-type epicuticular wax show the potential of these kinds of characters for evaluating competing gene trees. Comprehensive surveys of these and other independent data will be necessary for making the best phylogenetic inferences among families of the Bromeliiflorae–Commeliniflorae–Zingiberiflorae lineage.

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Appendix. Specimens used for sources of DNA.

| Species | Family | Voucher/Source | Database accession[5] |
|---|---|---|---|
| *Aechmea chantinii* (Carrière) Baker | Bromeliaceae | *G. K. Brown 3156* (WYO) | L19978 |
| *Ananas comosus* Merrill | Bromeliaceae | UCRBG *s.n.*[1] | L19977 |
| *Catopsis montana* L. B. Smith | Bromeliaceae | *G. K. Brown 3155* (WYO) | L19976 |
| *Glomeropitcairnia penduliflora* Mez | Bromeliaceae | SEL 86-700[2] | L19975 |
| *Hechtia montana* Brandegee | Bromeliaceae | *A. Sanders 9174* (UCR) | L19974 |
| *Pontederia sagittata* C. Presl | Pontederiaceae | S. C. H. Barrett[3] | L20128 |
| *Puya dyckioides* Mez | Bromeliaceae | UCRBG 76-16[1] | L19973 |
| *Ravenala madagascarensis* Strel. | Strelitziaceae | UCRBG *s.n.*[1] | L20138 |
| *Stegolepis allenii* Steyerm. | Rapateaceae | RSA *s.n.*[4] | L19972 |
| *Tillandsia elizabethae* Rauh | Bromeliaceae | *A. Sanders 2638* (UCR) | L19971 |
| *Vellozia* sp. | Velloziaceae | SEL 85-19[2] | L19970 |

[1] University of California at Riverside Botanical Garden, living specimen.
[2] Marie Selby Botanical Garden, living specimen.
[3] Donated genomic DNA of *P. sagittata* from the University of Toronto.
[4] Rancho Santa Ana Botanic Garden, living specimen.
[5] GenBank accession numbers.

# NOTES ON MAGNOLIACEAE III: THE MAGNOLIACEAE OF CHINA[1]

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ABSTRACT

Five genera of Magnoliaceae occur in China; these and the 81 indigenous and 7 cultivated species they contain are described here. In *Magnolia*, 28 wild and 4 cultivated species are recognized. *Magnolia nitida* var. *robusta* is newly described, and *Magnolia lotungensis* is reduced to *Magnolia nitida* var. *lotungensis*. In *Manglietia*, 17 indigenous and 1 cultivated species are recognized. Section *Manglietiastrum* is transferred from *Magnolia* to *Manglietia*, and *Magnolia sinica* is renamed *Manglietia sinica*. *Manglietia forrestii* is reduced to *Manglietia fordiana* var. *forrestii*, *Manglietia kwangtungensis* is reduced to *Manglietia fordiana* var. *kwangtungensis*, and *Manglietia calcarea* is reduced to *Manglietia fordiana* var. *calcarea*. In *Kmeria*, one species is recorded for China. In *Michelia*, 34 indigenous and 1 cultivated species are recognized. Section *Tsoongiodendron*, based on *Tsoongiodendron* W. Y. Chun, is recognized with one species, *Michelia odora*; section *Paramichelia*, based on *Paramichelia* H. H. Hu, is recognized with one species in China. *Michelia elliptilimba* is newly described. *Michelia crassipes* is reduced to *Michelia figo* var. *crassipes*. In *Liriodendron* one indigenous and one cultivated species are recognized. An identification list of all the collections studied, as well as a bibliography of Chinese Magnoliaceae, is given at the end of the paper.

The first author collected specimens of Magnoliaceae over a period of several years in China, especially in Yunnan. Apart from describing many new species, he wrote his thesis (in Chinese) on the Magnoliaceae of China. Because he did not have the opportunity to study the types in Western herbaria, or enough collections from southern Asia outside China, his earlier work could only be preliminary.

The second author published on the generic delimitation of Magnoliaceae and gave an account of the genera and species occurring in Malesia (Nooteboom, 1985, 1987). The present publication is the result of a joint Dutch–Chinese cooperation spanning 18 months at the Rijksherbarium at Leiden.

Sadly, soon after Chen Bao Liang returned to China in May 1991, he died from cancer.

## TERMINOLOGY

A few terms are used in this study that are not familiar to all taxonomists. Pedicle is not a pedicel, but the internode, if present, between the uppermost bract and the perianth. Literally, a brachyblast is a short shoot. In Magnoliaceae it means the shoot that bears the flower: it is terminal in Magnolieae and axillar in Michelieae. In Magnolieae, however, this character is called a peduncle because often it is longer. Innovations are the youngest parts of the twigs, often including stipules, that are still growing.

A list (List 1) of taxa and keys in the order in which they appear in the text follows the Bibliography. The numbering system in the text corresponds to that of List 1, Page 1096.

**Magnoliaceae** A.L. de Jussieu, Gen. Pl. 280. 1789 (Magnoliae).

Trees or shrubs, glabrous, or with an indumentum of single hairs. Leaves spirally arranged, simple, entire or 2–10-lobed, penninerved, evergreen or deciduous; stipules present, at first enclosing and protecting the buds, early caducous and leaving an annular scar around the node. Flowers terminal or pseudoaxillary on a short shoot (brachyblast) in the axils of the leaves, bisexual, rarely unisexual. Brachyblast or peduncle bearing 1 or more caducous spathaceous bracts, which leave annular scars. The highest bract either directly below the perianth or a pedicle present between bract and perianth. Perianth spiral or spirocyclic,

[1] We thank the directors and curators of P, K, E, and BM for the opportunity to study their collections and of the following herbaria for sending collections on loan: A, BM, E, GXMI, IBSC, K, KUN, LBG, MO, NY, P, PE, SYS, US, W. We thank the Dutch minister of Science and Education for providing, in the framework of the Chinese-Dutch Scientific Cooperation, the funds for Chen Bao Liang to spend 18 months in the Netherlands.

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undifferentiated or differentiated into a (pseudo-) calyx and corolla, perianth members 6 or more, free, imbricate. Stamens numerous, free, spirally arranged; filaments short or ± elongated; anthers linear, 2-locular dehiscing introrsely, latrorsely, or rarely extrorsely; connective usually ± produced into an appendage. Gynoecium sessile or stipitate (and then a gynophore present); carpels numerous to few (rarely one), spirally arranged, free or sometimes concrescent; ovules 2 or more, biseriate on the ventral suture. Fruit apocarpous, sometimes syncarpous; fruiting carpels (follicles) opening along the dorsal and/or ventral suture, or circumscissile, rarely indehiscent. Seeds 1 or more in each fruiting carpel, large, in dehiscent carpels with arilloid testa and pendulous from the elongated spiral vessels of the funiculus (in *Liriodendron*, with indehiscent fruits, adherent to the endocarp and not arilloid); endosperm copious, oily; embryo minute.

*Note 1.* Nooteboom (1985) provided an introduction to the family with chapters on anatomy, embryology, phytochemistry, palynology, morphology, and subdivision of the family. Dandy (1927a) gave an account of the genera, which he emended in Hutchinson (1964a) and Praglowski (1974). Praglowski (1974) gave an account of the pollen. The cultivated species were extensively treated by Treseder (1978).

*Note 2.* As in many other families, the delimitation of species in Magnoliaceae is often difficult because of high variability. Because recently many more collections, and also types of species that were described before World War II, became available, many species could be reduced to synonymy. It should be kept in mind that even within populations variability is high. For example, *Magnolia sprengeri* Pampanini, when grown from seed, displays much variability. The beautiful *Magnolia* var. *diva* is vegetatively propagated because the seedlings often are disappointing, showing a spectrum of offspring with not always attractive flowers. Several botanists would be inclined to describe these seedlings and their mother tree as many different species.

KEY TO THE GENERA OF MAGNOLIACEAE

1. Leaves 2–10-lobed, the apex truncate or widely emarginate; anthers extrorse; fruits samaroid. ..... **V.** *Liriodendron*
1. Leaves entire or occasionally 2-lobed or emarginate; anthers introrse or latrorse; follicles dehiscent or circumscissile, not samaroid. ..... 2
2(1). Growth monopodial; flowers on brachyblasts in the axils of the leaves; gynoecium distinctly stipitate. ..... **IV.** *Michelia*
2. Growth sympodial; flowers terminal on the twigs. ..... 3
3(2). Flowers unisexual; tepals 6–7, subequal. ..... **III.** *Kmeria*
3. Flowers bisexual or androdioecious; tepals 9 or more, sometimes the outer whorl calyxlike. 4
4(3). Ovules 4 or more in each carpel; the hair base replaces a normal epidermal cell, so that the loss of a hair leaves a pore in the cutical membrane. ..... **II.** *Manglietia*
4. Ovules 2 in each carpel (4 in *Magnolia kachirachirai*, 2–5 in *Magnolia cathcartii*), sometimes 4 in the lower carpels; the hair base consists of at least two epidermal cells, and a hair does not leave a pore after it is shed. ..... **I.** *Magnolia*

## MAGNOLIACEAE subfamily MAGNOLIOIDEAE

Leaves entire or occasionally 2-lobed at the apex; stipules free from the petiole or adnate to it. Anthers introrse or latrorse. Follicles longitudinally dehiscent or circumscissile and then at least the base remaining adnate to the torus, free or concrescent into a syncarp. Testa free from the endocarp, externally arilloid.

TRIBES

Tribe **Magnolieae**

Growth sympodial (flowers terminal on the twigs). Follicles free or concrescent. Genera: *Magnolia*, *Manglietia*, and *Kmeria*.

Tribe **Michelieae** Law Yuh-wu, Acta Phytotax. Sinica 22: 106. 1984.

Growth monopodial (flowers arising on brachyblasts in the axils of the leaves). Genera: *Elmerrillia* Dandy, with four species in Malesia, none in China, and *Michelia* L. (See page 1052.)

TRIBE MAGNOLIEAE

**I. Magnolia** L., Sp. Pl. 535. 1753. TYPE SPECIES: *Magnolia virginiana* L. (eastern United States).

*Talauma* Juss., Gen. Pl. 281. 1789. *Magnolia* sect. *Talauma* Baill., Adansonia 7: 3, 66. 1866. *Magnolia* subg. *Talauma* Pierre, Fl. For. Cochinch. 1: sub t. 1. 1880. TYPE SPECIES: *Talauma plumierii* (Schwartz) A. DC. (*Magnolia plumierii* Schwartz).

*Aromadendron* Blume, Bijdr.: 10. 1825. *Talauma* sect. *Aromadendron* Miq., Ann. Mus. Bot. Lugd.-Bat. 4: 70. TYPE SPECIES: *Aromadendron elegans* Blume = *Magnolia elegans* (Blume) H. Keng.

*Blumia* Nees, Flora 8: 152. 1828 nom. rejec., non *Blumea* DC., nom. cons. *Magnolia* sect. *Blumia* (Nees) Baill., Adansonia 7: 2. 1866. TYPE SPECIES: *Talauma*

*candollii* Blume = *Magnolia candollii* (Blume) H. Keng.

*Yulania* Spach, Hist. Natur. Veget., Phanerog. 7: 462. 1839. TYPE SPECIES: *Yulania conspicua* Spach = *Magnolia heptapeta* (Buchoz) Dandy.

*Tulipastrum* Spach, Hist. Natur. Veget., Phanerog. 7: 481. 1839. TYPE SPECIES: *Magnolia acuminata* L.

*Lirianthe* Spach, Hist. Natur. Veget. Phanerog. 7: 485. 1839. TYPE SPECIES: *Lirianthe grandiflora* Spach = *Magnolia pterocarpa* Roxb.

*Buergeria* Siebold & Zucc., Abh. Math.-Phys. Cl. Kon. Bayer. Ak. Wiss. 4, 2: 186. 1846. TYPE SPECIES: *Buergeria stellata* Siebold & Zucc. = *Magnolia stellata* (Siebold & Zucc.) Maxim.

*Alcimandra* Dandy, Kew Bull. 1927: 260. 1927. TYPE SPECIES: *Alcimandra cathcartii* (Hook. f. & Thomson) Dandy = *Magnolia cathcartii* (Hook f. & Thomson) Noot.

*Svenhedinia* Urban, Repert. Spec. Nov. Regni Veg. 24: 3. 1927. TYPE SPECIES: *Svenhedinia minor* (Urban) Urban (*Talauma minor* Urban).

*Parakmeria* Hu & Cheng, Acta Phytotax. Sin. 1(2): 1. 1951. TYPE SPECIES: *Parakmeria omeiensis* Hu & Cheng (= *Magnolia omeiensis* (Hu & Cheng) Dandy).

*Micheliopsis* H. Keng, Quart. J. Taiwan Mus. 8: 207, t. 345. 1955. TYPE SPECIES: *Micheliopsis kachirachirai* (Kaneh. & Yamam.) H. Keng = *Magnolia kachirachirai* (Kaneh. & Yamam.) Dandy.

*Dugandiodendron* Lozano-Contreras, Caldasia 11: 33. 1975. TYPE SPECIES: *Dugandiodendron mahechae* Lozano.

Trees or shrubs, stipules adnate to or free from the petiole. Flowers terminal, solitary, bisexual. Tepals 9–21, 3–5-merous, subequal or more rarely the outer whorl forming a calyx. Anthers introrse to latrorse; connective produced into a longer or shorter appendage or rarely unappendaged. Gynoecium sessile or in some species stipitate; carpels many to few, usually free but not connate in *Magnolia* subg. *Talauma*, in young fruits of *Magnolia* sect. *Gynopodium*, and in some other species. Follicles free, crowded, dehiscent along the dorsal suture; in *Magnolia* subg. *Talauma* the basal parts of the mature carpels staying adnate to the torus, the apical parts falling and thus exposing the seeds which hang from the lengthened funiculus, sometimes the apical parts during or before falling dorsally dehiscing; in some species of *Magnolia* sect. *Gynopodium* the carpels are connate but tear apart when maturing and dehisce dorsally. Ovules generally two in each carpel, rarely 3 or 4 in the lower carpels, in a few species to 4 or 5 in all carpels. Ripe seeds often hanging from the funicles, which lengthen through uncoiling of the spiral vessels.

*Distribution.* About 120 species, of which ca. one-third grow in the New World from southeastern North America to southern Brazil and the West Indies, the remainder in temperate and tropical Southeast Asia from the Himalayas to China, Japan, and Malesia.

KEY TO THE SUBGENERA AND SECTIONS OF *MAGNOLIA*

1. Fruits at least finally consisting of free follicles, which dehisce along the dorsal suture; stipules free from the petiole or connate to it; anthers introrse, sublatrorse or latrorse; plant evergreen or deciduous; midrib of leaves usually impressed, rarely prominent above. ..... 2
1. Fruits with connate carpels, when mature the apical parts of them circumscissile and falling, dehiscing along the dorsal suture, the basal parts remaining attached to the torus; stipules adnate to the petiole up to its apex; anthers introrse; plant evergreen; midrib of leaves prominent for the whole length (in the absence of fruits this section cannot be distinguished from section *Gwillimia*). ..... **Ic.** Subgenus *Talauma* **1.** Section *Blumiana*

2(1). Anthers dehiscing laterally or sublaterally; flowers precocious and/or with a much reduced calyxlike outer whorl of tepals; plant deciduous; fruit cylindric or oblong, usually ± distorted. **Ib.** Subgenus *Yulania*. ..... 3
2. Anthers dehiscing introrsely; flowers neither precocious nor with a much reduced (calyxlike) outer whorl of tepals; plant evergreen or deciduous. **Ia.** Subgenus *Magnolia*. ..... 5

3(2). Tepals subequal; flowers appearing before the leaves, white to rose or purple. ..... **Ib-1.** Section *Yulania*
3. Tepals very unequal, those of the outer whorl forming a calyx; flowers appearing before, together, or after the leaves. ..... 4

4(3). Flowers appearing before the leaves; inner (large) tepals white, sometimes tinged with rose or purple. ..... **Ib-2.** Section *Buergeria*
4. Flowers appearing together or after the leaves; inner tepals purple or green to yellow. ..... **Ib-3.** Section *Tulipastrum*

5(2). Stipules adnate to the petiole, leaving a scar on its surface; plants evergreen or deciduous; gynoecium sessile. ..... 6
5. Stipules free from the petiole, the latter unscarred; plants evergreen; gynoecium stipitate. ..... 8

6(5). Plants evergreen; flower buds at first enclosed in one or more spathaceous bracts, which leave as many annular scars on the peduncle. ..... **Ia-1.** Section *Gwillimia*
6. Plants deciduous; flower buds at first enclosed in a single spathaceous bract, which leaves a single annular scar on the peduncle. ..... 7

7(6). Leaves crowded into false whorls at the ends of the twigs, usually large or very large; connective of anthers produced into a short or long appendage. .. **Ia-2.** Section *Rytidospermum*
7. Leaves not crowded into false whorls at the end of the twigs; connective of anthers not produced into an appendage, blunt or retuse. ..... **Ia-3.** Section *Oyama*

8(5). Carpels usually with 2–5 ovules; flowers bisexual; fruits cylindrical, 1–4 seeds in each follicle; stamens with short filament and very long anther, hiding the gynoecium; at least twigs hairy. ..... **Ia-5.** Section *Alcimandra*
8. Carpels usually with 2 ovules, rarely with 4;

flowers androdioecious; plant entirely glabrous; anthers much shorter. ..... **Ia-4.** Section *Gynopodium*

KEY TO THE SPECIES OF *MAGNOLIA*
(primarily based on floral characters)

1. Leaves crowded at the end of the branchlets in false whorls, glaucous beneath. ..... 2
1. Leaves evenly distributed. ..... 3
2(1). Twigs and stipules glabrous; young leaves with rather long, crisped brown hairs beneath, base rounded, apex mucronate; pedicle 13 mm; outer tepals oblong-elliptic; inner tepals 11–13 cm long; stamens 14–17 mm long; gynoecium cylindric. ..... 9. *Magnolia rostrata*
2. Twigs and stipules hairy; leaves scattered, colorless hairy beneath, base cuneate, apex rounded or acute; pedicle 2–6 mm; outer tepals obovate; inner tepals 8–10 cm long; stamens 30–40 mm long; gynoecium ovoid. ..... 8. *Magnolia officinalis*
3(1). Anthers dehiscing laterally or sublaterally. 4
3. Anthers dehiscing introrsely. ..... 13
4(3). Tepals very unequal, outer tepals 0.8–2.7 cm long. ..... 5
4. Tepals subequal, outer tepals 5–14 cm long. 7
5(4). Inner tepals 4–5 cm long; tree to 12 m high; outer tepals 8–11 mm. ..... 25. *Magnolia biondii*
5. Inner tepals 5.5–10 cm long; shrub or treelet to 3–10 m high; outer tepals 10–27 mm. ..... 6
6(5). Leaves glabrous to pubescent with long, undulate, colorless hairs beneath; leaf base attenuate-cuneate; flowers appearing together or after the leaves, purple or red; filaments 2 mm long; peduncle 6–8 mm thick ..... 29. *Magnolia quinquepeta*
6. Leaves with fine, straight, colorless hairs beneath; leaf base cuneate or narrowly cuneate; flowers appearing before the leaves, white; filaments 3 mm long; peduncle 4–5 mm thick. ..... 26. *Magnolia cylindrica*
7(4). Gynoecium 8–15 mm high. ..... 8
7. Gynoecium 20–40 mm high. ..... 9
8(7). Twigs yellow-, black-, or gray-brown; leaves not glaucous beneath, reticulation coarse; flower purple or red. ..... 22. *Magnolia sargentiana*
8. Twigs yellowish to green turning reddish brown; leaves glaucous beneath, reticulation fine; flower white. ..... 20. *Magnolia dawsoniana*
9(7). Peduncle 24–30 × 7–10 mm. ..... 19. *Magnolia campbellii*
9. Peduncle 2–20 mm long. ..... 10
10(9). Twigs hairy at least when young. ..... 21. *Magnolia heptapeta*
10. Twigs glabrous. ..... 11
11(10). Stamens 9–10 mm long; leaf apex acuminate or acute ..... 18. *Magnolia amoena*
11. Stamens 15–17 mm long; leaf apex rounded or short-acuminate. ..... 12
12(11). Filaments 4 mm long; shrub to 7 m high; terminal winter buds long-hairy, sericeous; nerves in 8–12 pairs; leaf base broadly cuneate or rounded; flowers appearing before the leaves, purple or red. ..... 24. *Magnolia zenii*
12. Filaments 5–7 mm long; tree up to 20 m high; terminal winter buds densely villous; nerves in 6–8 pairs; leaf base cuneate or narrowly cuneate; flowers appearing together or after the leaves, white. ..... 23. *Magnolia sprengeri*
13(3). Stipules free; gynoecium stipitate. ..... 14
13. Stipules adnate to petiole; gynoecium not stipitate. ..... 20
14(13). Gynoecium exserted from stamens. ..... 15
14. Gynoecium entirely hidden within androecium. ..... 17
15(14). Peduncle 3–4 mm thick; leaves elliptic or obovate, base cuneate. ..... 14. *Magnolia kachirachirai*
15. Peduncle 5–6 mm thick; leaves ovate or narrowly elliptic, base broadly cuneate, narrowly cuneate, or rounded ..... 16
16(15). Midrib of leaf not prominent above; leaves narrowly elliptic, base narrowly cuneate; connective appendage 1.5 mm long; filaments 7 mm; outer tepals oblong. ..... 16. *Magnolia omeiensis*
16. Midrib of leaf prominent above, at least toward base; leaves ovate, base broadly cuneate or rounded; connective appendage 2–4 mm long; filaments 1–3 mm; outer tepals obovate or spathulate. ..... 15a. *Magnolia nitida* var. *nitida*
17(15). Outer tepals 5.5–6 cm long; plant hairy at least in innovations; twigs hairy at least when young; stipules pubescent; leaf base broadly cuneate or rounded, reticulation of leaf fine; petiole hairy; peduncle 2 mm thick; inner tepals 5.5 cm long, 25 mm broad. ..... 17. *Magnolia cathcartii*
17. Outer tepals 2.5–3.8 cm long; plant entirely glabrous; leaf base cuneate or narrowly cuneate, reticulation of leaf coarse; peduncle 5–9 mm thick; inner tepals 2.2–4.2 cm long, 1.2–18 mm broad. ..... 18
18(17). Outer tepals 3.8 cm long; leaf base narrowly cuneate, midrib not prominent above; outer tepals oblong; inner tepals 3.5–4.2 cm long. ..... 16. *Magnolia omeiensis*
18. Outer tepals 2.5–3 cm long; leaf base cuneate, midrib prominent above, at least toward base; outer tepals ovate; inner tepals 2.2–3 cm long. ..... 19
19(18). Nerves in 8–15 pairs; reticulation distinct; connective appendage 0.5 mm long; gynoecium narrowly ovoid; scars of perianth and stamens along torus under fruit 6–7 mm long; fruiting twigs ca. 8 mm thick. ..... 15c. *Magnolia nitida* var. *robusta*
19. Nerves in 9–13 pairs; reticulation rather obscure; connective appendage 2–4 mm long; gynoecium ovoid; scars of perianth and stamens along torus under fruit 2–4 mm long; fruiting twigs 4–6 mm thick. ..... 15b. *Magnolia nitida* var. *lotungensis*
20(13). Gynoecium hairy; reticulation fine. ..... 21

20. Gynoecium glabrous; reticulation coarse. 23
21(20). Carpels 55–64; twigs densely appressed, yellow, woolly; leaf base acute to rounded, rarely cordate; gynoecium ovoid. ..... 4. *Magnolia delavayi*
21. Carpels 15–24; twigs pubescent or silky; leaf base broadly to narrowly cuneate; gynoecium narrowly ovoid or ellipsoid. ..... 22
22(21). Leaves not glaucous beneath; twigs colorless to yellowish pubescent; peduncle slender; connective appendage triangular; gynoecium ellipsoid; follicles glabrous. ..... 2. *Magnolia championii*
22. Leaves glaucous beneath; twigs silky; peduncle stout; connective appendage short-pointed; gynoecium narrowly ovoid; follicles hairy. ..... 1. *Magnolia albosericea*
23(20). Peduncle hairy; plant deciduous; connective of anther not produced into an appendage, retuse or blunt. ..... 24
23. Peduncle glabrous; plant evergreen; connective produced into a short or long appendage. ..... 27
24(23). Gynoecium 23–25 mm high. ..... 10. *Magnolia globosa*
24. Gynoecium 13–20 mm high. ..... 25
25(24). Leaves not glaucous beneath; leaf apex rounded or mucronate; pedicle 13–17 mm; inner tepals ovate. ..... 12. *Magnolia sinensis*
25. Leaves glaucous beneath; leaf apex acuminate or acute; pedicle 2–7 or 8–15 mm; inner tepals obovate, spathulate, or oblong. 26
26(25). Leaves ovate or narrowly ovate; twigs villous; stipules silky; reticulation coarse but distinct; outer tepals elliptic; filaments 2 mm long; gynoecium ovoid or cylindric; fruiting peduncles 3–4.5 cm long. ..... 13. *Magnolia wilsonii*
26. Leaves obovate; twigs pubescent; stipules pubescent or sparsely hairy; reticulation rather obscure; outer tepals obovate; filaments 3 mm long; gynoecium ellipsoid; fruiting peduncles 6.2–7 cm long. ..... 11. *Magnolia sieboldii*
27(23). Leaves 2.5–5 cm broad, midrib not prominent above; petiole 5–15 mm; peduncle 14–20 mm long. ..... 3. *Magnolia coco*
27. Leaves 8–22 cm broad; midrib prominent above at least toward base; petiole 25–110 mm; peduncle 23–120 mm long. ..... 28
28(27). Plant hairy at least in innovations. ..... 29
28. Plant glabrous. ..... 30
29(28). Pedicle absent; connective appendage 3 mm long; filaments 3 mm long; gynoecium ellipsoid; fruits with connate carpels, when mature the apical parts of the carpels circumscissile and falling, dehiscing along the dorsal suture or not, the basal parts remaining adnate to the torus; fruits ellipsoid. ..... 30. *Magnolia candollii* var. *obovata*
29. Pedicle present; connective appendage 1 mm long; filaments 1–2 mm long; gynoecium narrowly ovoid; fruits ovoid to ovoid-cylindric, at least finally consisting of free carpels which dehisce along the dorsal suture. ..... 5. *Magnolia henryi*
30(28). Peduncle 5–13 mm thick; tree to 25 m high; leaf apex rounded or short-acuminate; outer tepals thick-fleshy; gynoecium ellipsoid. ..... 30. *Magnolia candollii* var. *obovata*
30. Peduncle 4 mm thick; shrub to 3 m high; leaf apex acuminate; outer tepals thin-coriaceous; gynoecium narrowly ovoid. ..... 6. *Magnolia phanerophlebia*

## Key to the Species of *Magnolia*
(primarily based on fruit characters)

1. Fruits with connate carpels, when mature the apical parts of the carpels circumscissile and falling, dehiscing along the dorsal suture or not, the basal parts remaining adnate to the torus. ..... 2
1. Fruits at least finally consisting of free carpels which dehisce along the dorsal suture. 3
2(1). Tree to 25 m high; apex of leaf rounded or short-acuminate; peduncle 5–13 mm thick. ... 30. *Magnolia candollii* var. *obovata*
2. Shrub or treelet to 3 m high; apex of leaf acuminate; peduncle 4 mm thick (fruits not known). ..... 6. *Magnolia phanerophlebia*
3(1). Stipules free; gynoecium stipitate. ..... 4
3. Stipules adnate to petiole; gynoecium not stipitate. ..... 10
4(3). Midrib of leaf not prominent above. ..... 5
4. Midrib of leaf, at least toward base, prominent above. ..... 7
5(4). Twigs hairy at least when young; stipules pubescent; base of leaf broadly cuneate or rounded, apex acuminate, reticulation distinct, fine, petiole hairy. ..... 17. *Magnolia cathcartii*
5. Twigs and stipules glabrous; base of leaf cuneate or narrowly cuneate, apex short-acuminate or acute, reticulation rather obscure, coarse, petiole glabrous. ..... 6
6(5). Leaves narrowly elliptic, base narrowly cuneate (fruits not known). ..... 16. *Magnolia omeiensis*
6. Leaves elliptic or obovate, base cuneate. ... 14. *Magnolia kachirachirai*
7(4). Leaves ovate. ..... 8
7. Leaves elliptic or narrowly elliptic. ..... 9
8(7). Leaves 7–16.5 cm long, reticulation distinct, base cuneate, apex rounded, acuminate, or acute, petiole 16–47 mm; fruiting twigs ca. 8 mm thick. ..... 15c. *Magnolia nitida* var. *robusta*
8. Leaves 6–12(–14) cm long, reticulation rather obscure, base broadly cuneate or rounded, apex short-acuminate, petiole 15–25 mm; fruiting twigs 5–6(–8) mm thick. ..... 15a. *Magnolia nitida* var. *nitida*
9(7). Fruiting twigs ca. 8 mm thick; leaves 7–16.5 cm long, reticulation distinct, petiole 16–47 mm; scars of perianth and stamens along torus under fruit 6–7 mm long. ..... 15c. *Magnolia nitida* var. *robusta*
9. Fruiting twigs 4–5(–6) mm thick; leaves 6–11 cm long, reticulation rather obscure, petiole 15–20 mm; scars of perianth and stamens along torus under fruit 2–4 mm long. .. 15b. *Magnolia nitida* var. *lotungensis*

10(3). Leaves crowded in false whorls terminal on the branchlets. ..... 11
10. Leaves evenly distributed. ..... 12
11(10). Twigs glabrous; stipules glabrous; young leaves beneath with brown hairs, base rounded, apex mucronate; pedicle 13 mm; fruit cylindric, 12–20.5 cm long, follicles with a beak of 6–8 mm. ..... 9. *Magnolia rostrata*
11. Twigs hairy at least when young; stipules sparsely hairy; young leaves beneath with colorless hairs, base cuneate, apex rounded or acute; pedicle 2–6 mm; fruit usually oblong-ovoid, 8–16 cm long, follicles with a beak of 1–3 mm. 8. *Magnolia officinalis*
12(10). Follicles hairy. ..... 13
12. Follicles glabrous. ..... 14
13(12). Twigs, stipules, and leaves glabrous, leaves not glaucous beneath, midrib at least toward base prominent above, reticulation coarse, petiole dilated at base; peduncle glabrous, 25 mm long, 4 mm thick; carpels 11 (fruits not known). 6. *Magnolia phanerophlebia*
13. Twigs hairy at least when young; stipules silky; leaves hairy beneath at least when young, glaucous beneath, midrib not prominent above, reticulation fine, petiole hairy, not dilated at base; peduncle hairy, 15 mm long, 6 mm thick; carpels 22. ..... 1. *Magnolia albosericea*
14(12). Leaves glaucous beneath. ..... 15
14. Leaves not glaucous beneath. ..... 19
15(14). Fruiting peduncles 6.2–7 cm long. ..... 16
15. Fruiting peduncles 1–4.5 cm long. ..... 17
16(15). Leaves elliptic or ovate, reticulation distinct; nerves in 8–11 pairs; stipules yellowish silky or brown-villous; fruits 2.5–9 × 2–2.5 cm. ..... 10. *Magnolia globosa*
16. Leaves obovate, reticulation rather obscured; nerves in 6–8 pairs; stipules pubescent or sparsely hairy; fruits 3–4 × 1.2–1.7 cm. ..... 11. *Magnolia sieboldii*
17(15). Fruiting peduncles 2–3 mm thick; stipules silky, reticulation of leaf coarse; stipular scars on petiole 10–25 mm long. ..... 13. *Magnolia wilsonii*
17. Fruiting peduncles 8–10 mm thick; stipules woolly, pubescent, or villous, reticulation of leaf fine, stipular scars 3–65(–85) mm long. 18
18(17). Evergreen tree; twigs and stipules densely appressed-woolly with yellowish hairs; pairs of lateral nerves of leaf 11–16(–21), petiole 45–65(–85) mm with stipular scar 40–65(–85) mm long; fruits ovoid. ..... 4. *Magnolia delavayi*
18. Deciduous tree; twigs glabrous to sparsely pubescent; stipules pubescent, pairs of lateral nerves of leaf 8–10, petiole 15–30 mm with stipular scar 3–4 mm long; fruits cylindric. ..... 20. *Magnolia dawsoniana*
19(14). Fruiting peduncles 2.5–9.5 cm long. ..... 20
19. Fruiting peduncles 1–2 cm long. ..... 27
20(19). Leaves 26–38(–65) cm long, midrib prominent above, at least toward base. ..... 21
20. Leaves 7–23 cm long, midrib not prominent above. ..... 22
21(20). Tree to 20 m high; plant hairy at least in innovations; stipules pubescent, stipular scars 55–110 mm long; apex of leaf rounded or acute; peduncle 6–10 mm thick; fruits ovoid to ovoid-cylindric, 7.5–14.5 × 3.5 cm. ..... 5. *Magnolia henryi*
21. Shrub to 3 m high; plant entirely glabrous; stipular scars 7–25 mm long, apex of leaf acuminate; peduncle 4 mm thick (fruits not known). ..... 6. *Magnolia phanerophlebia*
22(20). Peduncle 21–65 mm long. ..... 23
22. Peduncle 2–20 mm long. ..... 25
23(22). Shrub or tree to 5 m high; stipular scars 20–30 mm long; fruiting peduncles slender. ..... 12. *Magnolia sinensis*
23. Tree to 20–30 m high; stipular scars 2–7 mm long; fruiting peduncles stout. ..... 24
24(23). Twigs yellow-brown or black-brown to gray-brown, glabrous; petiole glabrous, stipular scars 2–5 mm long; fruits 3–20.5 cm long; flower purple or red; gynoecium 8–12 mm high. ..... 22. *Magnolia sargentiana*
24. Twigs purple-brown, sometimes brown to gray when dry, glabrous or pubescent; petiole glabrous or yellowish pubescent, stipular scars 3–7(–11) mm long; fruits 8.5–17 cm long; flower pink or white; gynoecium 25–40 mm high. ..... 19. *Magnolia campbellii*
25(22). Plant an entirely glabrous evergreen shrub, leaf apex acuminate; fruit ca. 3 cm long. ..... 3. *Magnolia coco*
25. Plant hairy at least in innovations, a deciduous tree, leaf apex rounded, short-acuminate, or acute; fruit 3–20.5 cm long. 26
26(25). Treelet to 7 m high; petiole hairy; leaf apex short-acuminate; peduncle 2–8 mm long. ..... 24. *Magnolia zenii*
26. Tree to 20 m high; petiole glabrous; leaf apex rounded or acute; peduncle under fruit 20–35 mm long. 22. *Magnolia sargentiana*
27(19). Twigs hairy at least when young. ..... 28
27. Twigs glabrous. ..... 33
28(27). Evergreen tree; fruits ovoid-elliptic; hairs colorless or yellowish. ..... 2. *Magnolia championii*
28. Deciduous tree; fruits cylindric, hairs colorless. ..... 29
29(28). Leaves appressed-pubescent with fine, short, straight hairs. ..... 26. *Magnolia cylindrica*
29. Young leaves different hairy beneath. ..... 30
30(29). Leaves obovate. ..... 31
30. Leaves elliptic, ovate, narrowly elliptic, or narrowly obovate. ..... 32
31(30). Shrub to 3.5 m high; twigs 2–4 mm diam., glabrous or sometimes hairy on a few nodes near the peduncles; leaf base attenuate-cuneate, apex acuminate or acute; fruits 3–6.5 × 1–2 cm. ..... 29. *Magnolia quinquepeta*
31. Tree to 20 m high; twigs 3–7 mm diam., finely appressed-pubescent when young; leaf base cuneate or rounded, apex short-acuminate; fruits 7.5–15 × 2.5–5 cm. ..... 21. *Magnolia heptapeta*

32(30). Shrub to 3.5 m high; leaves elliptic, base attenuate-cuneate; fruits 3–6.5 cm long. ..... 29. *Magnolia quinquepeta*
32. Tree to 12 m high; leaves ovate, narrowly elliptic, or narrowly obovate, base cuneate or rounded; fruits 6–14.5 cm long. ..... 25. *Magnolia biondii*
33(27). Leaves 31–36 × 9.5–17 cm. ..... 6. *Magnolia phanerophlebia*
33. Leaves 6–21.7 cm long. ..... 34
34(33). Plant evergreen, entirely glabrous. ..... 3. *Magnolia coco*
34. Plant deciduous, hairy at least in innovations. ..... 35
35(34). Leaf apex rounded or short-acuminate. ..... 36
35. Leaf apex acuminate or acute. ..... 37
36(35). Treelet to 7 m high; leaf base broadly cuneate or rounded; nerves in 8–12 pairs; petiole 6–15 mm; fruits 5–20 cm long; flowers appearing before the leaves. ..... 24. *Magnolia zenii*
36. Tree to 20 m high; nerves in 6–8 pairs; leaf base (narrowly) cuneate; petiole 10–35 mm; fruits 6–10 cm long; flowers appearing together or after the leaves. ..... 23. *Magnolia sprengeri*
37(35). Fruiting peduncles 4.1–6 mm thick. ..... 38
37. Fruiting peduncles 3–4 mm thick. ..... 39
38(37). Shrub to 3.5 m high; leaves elliptic or obovate, base attenuate-cuneate; stipular scars the entire length of the petiole; fruits 3–6.5 cm long; flowers appearing together or after the leaves. ..... 29. *Magnolia quinquepeta*
38. Tree to 12 m high; leaves ovate, narrowly elliptic, or narrowly obovate, base cuneate or rounded; stipular scar only at the base of the petiole; fruits 6–14.5 cm long; flowers appearing before the leaves. ..... 25. *Magnolia biondii*
39(37). Shrub to 3 m high; stipular scars as long as petiole, 3–15 mm long; leaf with 8–10 pairs of lateral nerves, base attenuate-cuneate; flowers appearing together or after the leaves. ..... 29. *Magnolia quinquepeta*
39. Tree to 12 m high; stipular scars adnate to base of petiole, 1–3 mm long; leaf with 10–13 pairs of lateral nerves, base cuneate, somewhat oblique; flowers appearing before the leaves. ..... 18. *Magnolia amoena*

## Ia. **Magnolia** subgenus **Magnolia**

Anthers dehiscing introrsely. Flowers neither precocious nor with a much reduced (calyxlike) outer whorl of tepals. Leaves evergreen or deciduous.

### Ia-1. **Magnolia** section **Gwillimia** A. DC., Syst. Nat. 1: 455, 548. 1817. TYPE SPECIES: *Magnolia coco* (Lour.) DC.

Evergreen shrub or tree. Stipules adnate to petiole to its apex. Leaves evenly distributed; midrib prominent above, at least toward base, or not prominent above. Flowers bisexual; tepals subequal. Outer tepals coriaceous; connective produced into a short or long appendage; anthers dehiscing introrsely. Gynoecium not stipitate. Number of ovules per carpel 2, sometimes 4 in the lower carpels. Scars of bracts 1–4. Fruits at least finally consisting of free follicles, which dehisce along the dorsal suture; follicles short-beaked, beak not dorsally flattened.

KEY TO THE SPECIES OF *MAGNOLIA* SECTION *GWILLIMIA*

1. Gynoecium hairy; reticulation of leaf fine. ..... 2
1. Gynoecium glabrous; reticulation of leaf coarse. 4
2(1). Leaves not glaucous beneath; twigs colorless to yellowish pubescent; peduncle slender; gynoecium ellipsoid. ..... 2. *Magnolia championii*
2. Leaves glaucous beneath; twigs white silky or yellowish woolly; peduncle stout; gynoecium ovoid or narrowly ovoid. ..... 3
3(2). Petiole 4–8.5 cm long; carpels 55–64; twigs and stipules yellowish woolly; leaf base acute to cordate, apex acute; outer tepals oblong; connective appendage of anthers triangular; gynoecium ovoid, fruits ovoid, follicles glabrous. ..... 4. *Magnolia delavayi*
3. Petiole 1–3.5 cm long; carpels ca. 22; twigs and stipules silky; leaf base cuneate or narrowly cuneate, apex acuminate; outer tepals elliptic; connective appendage of anthers short pointed; gynoecium narrowly ovoid; fruits obovoid or ellipsoid; follicles hairy. ..... 1. *Magnolia albosericea*
4(1). Leaves 10–17 cm long, 2.5–5 cm broad, midrib not prominent above, pairs of lateral nerves 8–10; petiole 5–15 mm; peduncle 14–20 mm long; gynoecium ellipsoid. ..... 3. *Magnolia coco*
4. Leaves 26–38 cm long, 8–17 cm broad, midrib prominent above, at least toward base, pairs of lateral nerves 13–20; petiole 30–110 mm; peduncle 23–50 mm long; gynoecium narrowly ovoid. ..... 5
5(4). Peduncle 6–10 mm thick; tree to 20 m high, hairy at least in innovations; stipules pubescent; apex of leaf rounded or acute; stipular scars 55–110 mm long. ..... 5. *Magnolia henryi*
5. Peduncle 4 mm thick; shrub to 3 m high, entirely glabrous, apex of leaf acuminate, stipular scars 7–25 mm long. ..... 6. *Magnolia phanerophlebia*

1. **Magnolia albosericea** Chun & C. H. Tsoong. Acta Phytotax. Sin. 9(2): 117. 1964. TYPE: China. Hainan: Poting, *F. C. How 72740* (holotype, IBSC; isotype, A).

Evergreen treelet to 8 m high; bark gray; young twigs, stipules, leaves beneath, midrib both sides, petioles, bracts, peduncles, and tepals outside white-sericeous, glabrescent; gynoecium yellow pubescent; young twigs ca. 4 mm diam. Stipules adnate

to the petiole, stipular scars nearly to the base of the blades, 9–34 mm long. Leaves coriaceous, dark green above, glaucous below, elliptic, narrowly elliptic or narrowly obovate-elliptic, 18–30(–40) × 6–9(–15) cm; apex acuminate, base cuneate to narrowly cuneate; midrib impressed above, prominent beneath; nerves fine, prominent below, in 15–20 pairs, reticulations finely netted, visible on both sides. Petiole 1–3.5 cm long. Peduncle ca. 1.5 × 0.6 cm. Tepals 9, the outer 3 long-elliptic, greenish, white sericeous outside at the midrib and the base, 4.5–5.5 × 1.3–2.5 cm, the inner tepals 6, very unequal, the innermost ones smaller than the others, spathulate-elliptic to broadly obovate, usually constricted basally into a short claw, 3–6.2 × 1.8–3.4 cm; stamens ca. 120, 1.5–2 cm long, anthers introrsely dehiscing, 6–8 mm long, connective appendage short-acute; gynoecium narrowly ovoid, ca. 20 mm high, carpels ca. 22, 8–13 mm long. Fruits ellipsoid to obovoid, 7–10 × 4–5 cm; mature carpels coriaceous, narrowly elliptic, brownish pubescent with short hairs and inconspicuously papillate, 2–2.5 cm long, beak recurved, 5–7 mm long. Seeds 14 × 6 mm.

*Distribution.* China and Vietnam. In CHINA: **Hainan, Baoting, Lingshui**: *Feng K.M. 72059; Zheng P. 12506; How F.C. 72059; 72740.*

*Ecology.* In evergreen broad-leaved forests along streams. Altitude: 500–800 m. Flowering April–May, fruiting August–September.

*Collector's notes.* Bark gray; leaves deep green, lustrous above, glaucous, green beneath; fruits green.

*Notes.* This species was treated as *Magnolia fistulosa* (Finet & Gagnep.) Dandy in W. Y. Chun (1963) and as *Magnolia champacifolia* Dandy ex Gagnep., nomen nudum, in Humbert (1938).

2. **Magnolia championii** Benth., Fl. Hongkong: 8. 1861. *Magnolia pumila* var. *championii* Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 36. 1905. *Magnolia lilifera* var. *championii* Pamp., Bull. Soc. Tosc. Ortic. 4(1): 136. 1916. TYPE: *Champion 37* (holotype, K).

*Magnolia fistulosa* (Finet & Gagnep.) Dandy, Notes Roy. Bot. Gard. Edinburgh 16: 124. 1928. *Talauma fistulosa* Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 31, t. 4b. 1905. TYPE: *Bon 3176* (lectotype, selected here, P).

*Magnolia paenetalauma* Dandy, J. Bot. 68, 206: 1930. TYPE: *Tsang & Fung 538 in Herb. Lingn. Univ. 18072* (holotype, BM; isotypes, K, IBSC, NY).

*Magnolia talaumoides* Dandy, J. Bot. 68: 208. 1930. TYPE: *Poilane 6370* (holotype, P).

*Magnolia tenuicarpella* Chang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 54. 1961. TYPE: *McClure 20099* (holotype, SYS).

*Magnolia odoratissima* Law & R. Z. Zhou, Bull. Bot. Res. (China), 6, 2: 139. 1986. TYPE: *R. Z. Zhou 0054* (holotype, IBSC).

Evergreen shrub or small tree to 11 m high; young twigs 3–5 mm diam., yellow-green, brown when dry, smooth, at first colorless to yellowish appressed-pubescent, finally glabrescent, or glabrous. Stipules adnate to the petiole, stipular scars to halfway to whole length of the petiole, 3–30 mm long. Leaves dark bright green, olive-green, to brown when dry, glabrous or pubescent with scattered hairs that are too minute to be visible above, somewhat pale green, glabrous or pubescent with long, straight, white, yellowish to brownish hairs, especially on the midrib and nerves beneath, thinly coriaceous to coriaceous, elliptic, narrowly obovate-elliptic to obovate, 8–17.5(–30) × 3.5–7(–10.5) cm; apex acute or acuminate to cuspidate with a 1.5–2.5-cm-long tip, base narrowly to broadly cuneate; midrib impressed above, nerves fine, prominent below when dry, in 8–14(–16) pairs, straight, anastomosing and meeting in a looped intramarginal vein at some distance from the margin, reticulations densely netted, visible on both sides. Petiole pubescent or glabrous, erect to slightly recurved, 6–30 mm long. Peduncles glabrous or yellowish pubescent, erect or slightly curved, 1–2(–4) × 0.3–0.5 cm, pedicles 3–4 mm long; bracts 2–3, white or yellowish pubescent outside. Flowers heavily fragrant; tepals 9, the outer 3 thinly coriaceous, greenish, oblong-elliptic to obovate, 3.5–6 × 2–3 cm, the inner tepals 6, white, broadly obovate to obovate-spathulate, basally with a short claw, fleshy, 4–5 × 2–4.5 cm; stamens white, 7–15 mm long, anthers dehiscing introrsely, connective appendage triangular, ca. 1 mm long, filaments 1–1.5 mm long; gynoecium ellipsoid, 1.5–2 × 0.5–0.8 cm, carpels 15–24, densely yellow pubescent, 8–10 mm or longer. Fruiting peduncles 14–17 × 3.5–5.5 mm, pedicles ca. 4 mm long. Fruits ovoid-elliptic, 4–6 cm long, ripe carpels 1–3 cm long, apex with a 2–3-mm-long beak; scars of perianth and stamens 5–7 × 5–7 mm. Seeds narrowly oblong or irregularly ovate, ca. 8–9 mm long.

*Distribution.* China and Vietnam. In CHINA. **Southern and southwestern Guangdong**: Ding Hu Shan, *Ting K.C. & K.L. Shi 1590*; Mao Ming, *Tang L. s.n.*; Shi Wan Da Shan, *Liang H.Y. s.n.* **Guangxi**: Da Ming Shan, *Chun S.H. 12003, Chen B.L. 86 G 7, Chen M.L. 3-5535, Cai C.X. 5465 29-V*; Dong Xing Xian, *Li T.Z. 1458*; Huan Jiang Xian, *Huan Jiang Exped. 4-3-1459.* **Guizhou**: Du Shan Xian, *Li Bo Exped. 1170.*

**Hainan**: *Liang H.Y. 63698, 64334, 64633, 64988, Wang C. 33359,* and many other collections. HONGKONG. **Happy Valley**: *Chang H.T. 86094, 86031, Champion 37, Bodinier E. 1221, Taam Y.W. 2149,* and several other collections. TAIWAN. **Tai Chung, Chi chi**, *Liao Jih-Ching 10085.* CHINA. **Southeast Yunnan**: *Chen B.L. 86 S 510, Chen B.L. 86 S 538, 86 S 507, 87 F 196, 87 F 222.*

*Ecology.* In evergreen broad-leaved forests. Altitude: 400–1,000 m. Flowering May–June; fruiting September–October.

*Uses.* Tree cultivated as an ornamental.

*Notes.* *Magnolia championii* is quite variable in habit, shape, and size of the leaves, measurement of the flowers, and number of the carpels. We doubted at first whether the species mentioned above were conspecific. However, after carefully comparing type specimens and other collections, we came to the conclusion that they are indeed. In fact, the differences are related to the distribution: in Guangdong the species usually is a shrub with smaller flowers and leaves that are somewhat cuspidate at the apex; in Hainan the species possesses relatively narrow, long leaves with a seemingly impressed midrib and nerves; in Yunnan it has broader leaves and bigger flowers. Finally, the Vietnamese *Magnolia fistulosa* and *Magnolia talaumoides* should be mentioned. The former is similar to *Magnolia championii* in all characters except its larger leaves and greater number of carpels. The latter differs from *Magnolia championii* by its glabrous twigs, leaves, and peduncles. There are arguments to support treating *Magnolia talaumoides* as a variety of *Magnolia championii*, but for the moment we refrain from that.

*Magnolia championii* was misidentified as *Talauma pumila* (Andr.) Blume by Champion (1851) and included in *Magnolia pumila* Andr. by F. Forbes & Hemsley (1886). It was included in *Magnolia coco* (Lour.) DC. by Rehder & E. Wilson (1913) and Merrill (1923).

3. **Magnolia coco** (Lour.) DC., Syst. Nat. 1: 459. 1817. *Liriodendron coco* Lour., Fl. Cochinch.: 347. 1790. *Talauma coco* (Lour.) Merr., Sp. Blancoan.: 12. 1918. TYPE: *Loureiro* (not seen).

*Magnolia pumila* Andr., Bot. Repos. 4: t. 226. 1802. *Talauma pumila* (Andr.) Blume, Fl. Javae, Magnoliaceae: 38, t. 12c. 1828. *Liriopsis pumila* (Andr.) Spach ex Baillon, Adansonia 7: 4. 1866. TYPE: t. 226 (Andr., 1802).

Evergreen shrub to small tree 2–4 m high; plant glabrous; bark gray; twigs shining green, brown-yellow when dry, smooth, ± angular. Stipules adnate to high on the petiole, stipular scars nearly up the entire length of the petiole, 5–15 mm. Leaves coriaceous, dark glossy green, usually olive green when dry above, greenish beneath, elliptic, narrowly elliptic, ovate-elliptic, to obovate-elliptic, 10–17 × 2.5–5 cm; apex long-acuminate, sometimes acute, base cuneate to broad-cuneate; margin slightly undulate; midrib not prominent on the upper surface; nerves in 8–10 pairs, curved upward and meeting in an intramarginal vein at some distance from the margin, reticulation coarsely netted, nerves and reticulation yellow to brown and prominent on the under surfaces. Petiole 5–15 mm long. Peduncles gray-black when dry, covered with a waxy substance, pendulous, with 3 bract scars, 1.4–2 cm long, pedicles 2–3 × 3–4 mm. Flowers nodding, subglobose, 3–4 cm diam., heavily scented, usually opening in the night; tepals 9, unequal, obovate, dorsal faces convex, the outer 3 greenish, thin coriaceous, 2–2.6 × 1.2–1.7 cm, the inner tepals 6, white, fleshy, oblong to obovate-oblong, 3–4 × 4 cm; stamens white, 5–7 mm long, anthers dehiscing introrsely, filaments 1.5–2 mm long, connective appendage rounded to acute; gynoecium obovoid-ellipsoid, ca. 1 × 0.7 cm, carpels 8–12, 5–6 mm long, styles short, torus with the scars of perianth and stamens 4–5 × 3–5 mm. Fruits can be seen occasionally, ca. 3 cm long, ripe carpels subligneous.

*Distribution.* China and northern Vietnam. In CHINA. **Fukien, Kushan**: *Chung H.H. 779; 8492.* **Guangdong**: Canton, *Gaudichaud Voy. sur la Bon 232*; Lofoushan, *Tsiang Y. 1757*; Lokchong, *Tso C.L. 20671*; Shiuchow, *To Kang Peng CCC herb. 2856*; Ting Wu Shan, *Chun W.Y. 6481 A.* **Guangxi**: He Pu, *Liang C.F. 33243.* **Guizhou**: *Esquirol 3061.* **Zhejiang**: Wenchow, *Ching R. C. 1904.* HONGKONG: *Kit Yock Chan 1352, Chun W.Y. 4520, Hu S.Y. 5393, 10194, 10201.* Also in Fujian anad Taiwan. Cultivated in Southeast Asia.

*Ecology.* In evergreen broad-leaved forest. Altitude: 600–900 m. Flowering April–October.

*Uses.* Used for medicinal purposes and to extract volatile oil; also grown as an ornamental.

*Note.* No original Loureiro specimen has been traced.

4. **Magnolia delavayi** Franchet, Pl. Delavay: 33, tt. 9–10. 1889. TYPE: *Delavay 2231* (holotype, P).

Evergreen tree to 18 m high and 25 cm diam., bark black-gray, becoming yellow-gray when dry, rough, fissured; young twigs dull green, densely appressed-woolly with yellowish hairs, provided with obvious orbicular and punctiform lenticels, old ones black-brown and glabrescent. Stipules covered with

same indumentum as young twigs, adnate to high on the petiole, stipular scars nearly to the end of the petiole, 4–6.5(–8.5) cm long. Leaves coriaceous, green, pubescent, glabrescent above, glaucous, densely appressed-woolly with curly, yellow hairs to glabrescent beneath, ovate, narrowly ovate to elliptic, 14.5–26(–30) × 7–15.5(–18) cm; apex acute, occasionally retuse, base acute to rounded, rarely cordate; midrib and nerves conspicuously elevated below, nerves in 11–16(–21) pairs, reticulation densely netted, prominent on both sides. Petiole at first densely yellowish pubescent, later glabrescent, 4–6.5(–8.5) cm long. Peduncles stout, pubescent, glabrescent, 1.2–2.5 × 0.7–0.9 cm, pedicle short, 1–5 mm long. Flowers slightly fragrant, usually fading one day after opening, creamy white, 15–20 cm diam., tepals 9(or 10), the outer 3 thin coriaceous, greenish, oblong, 6–8(–10) × 2.5–3(–4) cm, reflexed later, the inner tepals 6, white, spathulate obovate, fleshy, 7–9.5(–11) × 3–5 cm, the innermost tepals 3, usually erect and then enclosing androecium and gynoecium; stamens 1.5–2 cm long, anthers dehiscing introrsely, connective appendage triangular, 1.5–4 mm long, filaments 1–2 mm long; gynoecium ovoid, 1.5–2.2 × 1–1.2 cm, carpels 55–64, yellowish pubescent basally. Fruiting peduncles 1–4 × 0.8–1 cm, pedicles 2–5 × 8–10 mm. Fruits ovoid, 7–11 × 3–5 cm, ripe carpels narrowly elliptic, 2.5–4 cm long in the lower and 1.7–2 cm long in the upper carpels, with a 4–10-mm-long beak apically.

*Distribution.* CHINA. **Sichuan**: Hsiangyun distr., *Forrest G. 57*. **Yunnan**: throughout, Chenkang Hsien, *Forrest G. 27979*, *Wang C.W. 72469*; Yu long shan, Li kiang, *Wang C.W. 71760*; Huei-li Hsien, *Yu T.T. 1429*; Kien-shuei Hsien, *Tsai H.T. 53143*; Kouang yu ten (Langkong), *Delavay 2231*; Li-kiang Hsien, *Wang C.W. 71464*; Lunan Xian, Changhu, *Sino-Amer. Bot. Exped. 1630* and many other collections. Southwestern Guizhou.

*Ecology.* In broad-leaved forest. Altitude: 1,500–2,800 m. Flowering April–June; fruiting August–October.

*Uses.* Bark used for medicinal purposes, the tree as an ornamental.

5. **Magnolia henryi** Dunn, J. Linn. Soc. Bot. 35: 484. 1903. TYPE: *Henry 12782A* (lectotype, selected here, A; isolectotypes, E, MO, NY, US).

*Talauma kerrii* Craib, Kew Bull. 1922: 226. 1922. TYPE: *Kerr 5060* (K).

*Manglietia wangii* Hu, Bull. Fan. Mem. Inst. Biol. (Peiping) 8: 33. 1937. TYPE: *C. W. Wang 76888* (holotype, PE; isotypes, A, TIE).

Evergreen tree to 20 m high; young twigs brown-yellow, 5–7 mm diam., glabrous or sparsely yellowish pilose, smooth, ± angular. Stipules densely yellowish hairy, adnate to the petiole, scars up to the bases of the blades, 5.5–11 cm long. Leaves coriaceous, dark glossy green, glabrous above, green, glabrous or sparsely appressed-pubescent with straight, yellow-brown hairs beneath, obovate-oblong, oblong to ovate, 26–38(–65) × 8–13.5(–22) cm; apex rounded or acute, occasionally retuse, base cuneate, sometimes rounded; midrib and nerves prominently elevated below, nerves in 14–20 pairs; reticulation coarse, visible on both surfaces. Petiole glabrous or appressed-hairy, 5.5–11 cm long. Flower buds ovate; peduncles 2.3–5 × 0.6–1 cm, glabrous, usually recurved, covered with waxy substance, pedicles ca. 12 mm long; spathaceous bracts 2–3, glabrous; tepals 9, subsimilar, the outer 3 pale green outside, white inside, ovate-elliptic, the inner tepals 6, white, fleshy, obovate to spathulate, 5–6 × 2–3 cm; stamens 1.2–1.5 cm long, anthers introrsely dehiscing, connective appendage triangular, ca. 1 mm long, filaments 1–2 mm long; gynoecium long ovoid, 4–5 × 1.3–1.5 cm, carpels many; scars of perianth and stamens along the torus 1.5–1.7 × 1–1.3 cm. Fruiting peduncles 7–9.5 cm long × 7–10 mm. Fruits ovoid to ovoid-cylindric, 7.5–14.5 × 3.5 cm, ripe carpels 1.3–2 cm long, apically with beaks of 3–5 mm long. Seeds irregularly shaped, ca. 5–12 × 7 mm.

*Distribution.* China, Upper Burma, Thailand, Laos. In CHINA. **Southwestern Yunnan**: Xi Shang Ban Na, *Feng K.M. 22710*; Fo Hai, *Wang C.W. 76002*; Lang-tsang Hsien, *76518*; Lung-huk, Jenn-Yeh Hsien, *80116*; Meng Hai, *Li Y.H. 3607*; Meng La, *Tsai H.T. 59-10917*; Nan Chiao, *Wang C.W. 76888*; Szemoa, *Henry A 12782 A*.

*Ecology.* In evergreen broad-leaved forest. Altitude: 540–1,500 m.

*Collector's note.* Flowers white or ivory, very fragrant.

6. **Magnolia phanerophlebia** B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 107. 1988. TYPE: *B. L. Chen & C. N. Mai 87T001* (holotype, SYS).

Evergreen shrub or treelet ca. 3 m high and 6 cm diam., plant glabrous. Young twigs 5–7 mm diam., gray to yellow-gray when dry, terete, smooth. Stipules adnate to the base of the petiole, stipular scars 7–19(–25) mm long. Leaves coriaceous, dark green and shiny above, greenish beneath, obovate to elliptic, 31–34.5(–36) × 9.5–14(–17) cm; apex

acuminate, acumen 1–2 cm, base cuneate, decurrent with two ridges into the petiole; midrib conspicuously elevated beneath; nerves in (11–)13–17(–19) pairs, much impressed above, anastomosing and meeting in an intramarginal vein that is more prominent than the coarsely netted reticulation on both surfaces. Petiole obviously thickened toward its base, (1–)3–6(–7) cm. Peduncle recurved, ca. 2.5 × 0.4 cm; spathaceous bracts 3, one toward the base of peduncle and one at the base of perianth, the third at the middle of peduncle or higher. Tepals 8–9, subequal, the outer 3 greenish, thin coriaceous, the inner tepals 5–6, white, fleshy. Stamens numerous. Gynoecium narrowly ovoid, carpels ca. 11. Fruits not seen.

*Distribution.* CHINA. **Southeastern Yunnan**: Maguan, *Chen B.L. 87 T 1, 87 T 3.*

*Ecology.* In evergreen broad-leaved forest. Altitude 500–700 m.

*Notes.* The description is drawn from limited material with only flower buds. This species is quite similar to *Magnolia candollii* var. *obovata*, from which it differs by its shorter peduncles and fewer carpels. Because so far the mature flowers and fruits have not been gathered, we were unable to compare it with *Magnolia candollii* var. *obovata*; thus *Magnolia phanerophlebia* is temporarily maintained as a species here in section *Gwillimia*.

### Ia-2. **Magnolia** section **Rytidospermum**

Spach, Hist. Nat. Veget. Phanerog. 7: 474. 1839. TYPE: *Magnolia tripetala* L.

Deciduous trees. Stipules adnate to petiole. Leaves large, crowded at the end of the branchlets in false whorls; midrib not prominent above. Flowers bisexual; tepals subequal; connective produced into a short or long appendage; anthers dehiscing introrsely. Gynoecium not stipitate. Number of ovules per carpel 2, sometimes 4 in the lower carpels. Scars of bracts 1. Fruits at least finally consisting of free follicles, which dehisce along the dorsal suture.

KEY TO THE SPECIES OF *MAGNOLIA* SECTION *RYTIDOSPERMUM*

1. Twigs glabrous, yellow to purple-brown when dry ..... 2
1. Twigs densely appressed-hairy, soon glabrescent, yellow to yellowish gray, 8–14 mm diam.; filaments red, stout, 4 mm long. ..... 8. *Magnolia officinalis*
2. Twigs 6–8 mm diam., purple-brown, conspicuously supplied with semicircular to elliptic leaf scars; filaments crimson, ca. 12 mm long. ..... 7. *Magnolia hypoleuca*
2. Twigs 7–14 mm diam., yellow to purple-brown when dry, smooth, covered with a gray waxy substance; filaments 4–5 mm long. ..... 9. *Magnolia rostrata*

7. **Magnolia hypoleuca** Siebold & Zucc., Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4(2): 187. 1845. TYPE: *L-908-126-1201* (L).

*Magnolia hypoleuca* [var.] *β concolor* Siebold & Zucc., Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4, 2: 187. 1845. TYPE: *L-908-126-1103* (L).

Deciduous tree to 30 m high; bark gray, longitudinally fissured; young twigs 6–8 mm diam., purple-brown, glabrous, conspicuously supplied with semicircular to elliptic leaf scars; terminal winter buds large, ovoid-cylindric, ca. 4 cm long, glabrous and glaucous. Stipules glabrous, adnate to the base of the petiole, scars 1.5–2.5 cm long. Leaves crowded at the end of the twigs, thinly chartaceous, green, glabrous, sometimes pubescent along the midrib above, glaucous, pubescent with stout, long, crisped, colorless hairs everywhere as well as with slender, straight, colorless hairs along the midrib and nerves beneath, obovate, 20–38(–45) × 12–18(–20) cm; apex apiculate or short-acuminate, base broadly cuneate to obtuse; midrib and nerves prominently elevated below, nerves in 15–20 pairs, reticulation coarsely netted, obscured on both sides. Petiole glabrous to sparsely pubescent, lenticellate, 3–4.5 cm long. Flowers appearing after the leaves, cup-shaped, fragrant, 14–20 cm diam., peduncles glabrous, ca. 2.5 × 1 cm, pedicles ca. 5 × 8 mm; tepals 9–12, the outer 3 broadly oblong, greenish, pale reddish tinged, ca. 8 × 4 cm, the inner tepals 7–9, spathulate, creamy white, ca. 11 × 4.7 cm; stamens whitish, ca. 2.6 cm long, anthers introrsely dehiscing, connective appendage triangular, ca. 1 mm long, filaments crimson, ca. 12 mm long; gynoecium greenish, cylindric, ca. 3.5 × 1 cm, torus with the scars of perianth and stamens ca. 8 × 10 mm. Fruiting peduncles ca. 3.5 × 1 cm, pedicles 1.7 cm long. Fruits ovoid-cylindric, 12–13.5 × 4.5–6 cm; ripe carpels 1.5–2.5 cm long, apically with recurved beaks 5–10 mm long; scars of perianth and stamens along the torus ca. 2 × 1.2 cm.

*Distribution.* Native of Japan, cultivated in northern China.

*Uses.* Wood fine-textured, light and soft, generally used for construction work, furniture, musical instruments, and boards; tree grown as an ornamental because of its big and magnificent flowers.

*Note.* Ueda (1985, 1986) discussed the synonymy. For a long time the name *Magnolia obovata* Thunb., nom. illeg., was used, e.g., by Rehder & E. Wilson in Sargent (1913), Johnstone (1955), H. Hara (1977), Ohwi (1978), and Kitamura & Murata (1981) for this species. The species was named *Magnolia hoonoki*, nom. nudum, by Siebold (1830) and Millais (1927). More information on misapplied names used for this species follows here:

*Magnolia glauca* auct. non L.: Thunb. [var.] *β* Thunb., Fl. Jap.: 236. 1784b, only for the Japanese name Fo no Ki and the descr. *Magnolia obovata* [Thunb., Trans. Linn. Soc. London 2: 336. 1794a only for the Japanese name Fo no Ki and the descr. (*Thunberg 12885*, UPS) nom. illeg.; Mus. Nat. Acad. Upsal. 16: 137, sine descr. 1794b; Pl. Jap. Nov. Sp.: 8, 1824; sine descr.]. E. Wils., Gard. Chron. 39: 234. 1906.

*Magnolia longifolia* auct. non Sweet: Yanagida, J. Soc. Forest. (Japan) 16, 3: 268, t. 413. 1934. *Magnolia obovata* Thunb. var. *yanagidana* Hatusima, Acta Phytotax. Geobot. 4: 209. 1935. TYPE not known.

8. **Magnolia officinalis** Rehder & E. H. Wilson in Sarg., Pl. Wilson 1: 391. 1913. TYPE: *E. H. Wilson 652* (holotype, A; isotypes, E, GH, US).

*Magnolia officinalis* var. *biloba* Rehder & E. H. Wilson in Sarg., Pl. Wilson 1: 392. 1913. *Magnolia biloba* (Rehder & E. H. Wilson) Cheng & Law, Iconogr. Cormoph. Sinicorum 1: 787, t. 1574. 1972. *Magnolia officinalis* subsp. *biloba* (Rehder & E. H. Wilson) Cheng & Law in W. C. Cheng, Sylva Sinica 1: 449, t. 134. 1983. TYPE: *E. H. Wilson 1649* (holotype, A; isotypes, E, US).

*Magnolia officinalis* var. *pubescens* C. Y. Deng, J. Nanjing Inst. Forest. 1: 145. 1986. TYPE: *C. Y. Deng 84182* (not seen).

Deciduous tree to 20 m high, bark thick, gray, smooth; young twigs stout, 8–14 mm diam., yellowish to gray, sometimes brown, densely appressed-hairy, with short, straight to undulate, colorless to brown hairs, soon glabrescent, the old ones brownish gray; terminal buds large, narrowly ovoid, brown-hairy, 3.5–5.5 × 1–1.2 cm. Stipules membraneous to chartaceous, sparsely hairy with long hairs, scattered glandular punctate, adnate to the petiole, scars 0.5–2.7 cm long. Leaves large, thinly coriaceous, 7–8 crowded together at the top of the twigs, green, glabrous above, pale green, glaucous, scattered-pubescent with short, straight to slightly curly, colorless hairs as well as rather long, crisped, colorless hairs everywhere, later glabrescent beneath, obovate, 16.5–37.5(–46) × 9–20(–24) cm; apex acute, obtuse, emarginate to obcordate, base cuneate; both midrib and nerves prominently elevated, covered with slender, straight to undulate, colorless hairs below, nerves in 14–25(–40) pairs, reticulation coarsely netted, visible on both sides. Petiole stout, densely brown or gray hairy, glabrescent, 1.9–5 cm long. Flowers appearing with or after the leaves, white, sometimes flushed with purplish red, fragrant, 10–15 cm diam.; peduncles 3–5 × 0.5–0.8 cm, densely pubescent with long, straight, crisped, gray hairs, pedicles 2–6 mm long; tepals 9–12(–17), thick fleshy, the outer 3 pale green outside, obovate, usually reflexed, the inner tepals 6–9(–14), obovate to spathulate, 8–10 × 2.5–5 cm; stamens 3–4 cm long, anthers introrsely dehiscing, connective appendage triangular, ca. 1 mm long, filaments red, stout, 4–8 mm long; gynoecium ovoid, 2.5–3.5 × 1 cm; torus with the scars of perianth and stamens 1–1.8 × 1.2 cm. Fruiting peduncles glabrous to densely gray-hairy 3–5 × 0.5–0.8 cm. Fruits oblong-ovoid, occasionally cylindric, straight to slightly distorted by abortion of part of the carpels, 8–16 × 4.5–5 cm; ripe carpels 1–3 cm long, with 1–3-mm-long beaks at the apex; the scars of perianth and stamens along the torus ca. 1.4–2 × 1.5 cm. Seeds ovoid to irregularly shaped, ± compressed, 8–10 × 6–9 mm.

*Distribution.* CHINA. **Southern Anhui**: Chang Gon Shan, Wu Yuan, *Yieh P.C. 345*, *Ching R.C. 3227*; Chiuhwa Shan, *Sun S.C. 1293*; Wangshan, *Chow K.S. 126*. **Fujian**: *Ching R.C. 2519*. **Northern Guangdong**: Ruyuan, *Chen B.L. et al. 81001*. **Northern Guangxi**: Lin Gui, *Liang H.Y. 100218*; Long Sheng, *Huang D.A. 6034*; Hsi-Chang village, Ch'i-fen-shan, Kweilin distr., *Tsang W.T. 28495*. **Northern & northeastern Guizhou**: Shi Jian Xian, *Qiannan Exped. 3112*; Weining, *Tsiang Y. 9169*. **Southwestern Hunan**: Yang Shan, Changning Hsien, *Fan C.S. & Y.Y. Li 281*. **Western Hubei**: Chienshih Hsien, *Henry A 4886*, *Chow H.C. 1367*; Patung Hsien, *Chow H.C. 46*, *Wilson E.H. 652*, *Henry A 1475, 549, 3711*. **Jiangxi**: Kuling, Lotus Valley, *Chiao C.Y. 18759*; Ku-ling, *Chung H.H. & S.C. Sun 680*; Sa-tiu-hong, Yungshiu, *Tsiang Y. 10616*; Kinkiang, *Wilson E.H. 1649*. **Sichuan**: Kuan Hsien, *Wang F.T. 20441*; Mt. Omei, *Yu T.T. 517*, *Chiao C.Y. & C.S. Fan 436*; Wan Hsien, Mou-tao-chi, *Hwa C.T. 38*. **Xizang**: Moupin, *Werner E. s.n.* **Western & southern Zhejiang**: 50 li N of Sia chu, *Ching R.C. 1610*; Lungtsuan, *Ho Y.Y. 3201*; Mokanshan, *Meyer F.N. 1572*; Swen chi, southern Yentang, *Hu H.H. 93*; Tien tai shan, Huating, *Chiao C.Y. field no. 1050, herb. no. 14349*. The species is also reported from southern Shaanxi.

*Ecology.* In forest. Altitude: 300–1,300 m. Flowering May–June; fruiting August–October.

*Uses.* Bark, root-bark, flowers and seeds all used for medicinal purposes; seeds also for extraction of oil; wood yellowish brown, straight-grained and fine-textured, soft, used for construction, ve-

neer, furniture, and musical instruments. Because of its dense crown, large leaves, and beautiful flowers, the tree is grown as an ornamental.

*Collector's notes.* Leaves whitish beneath; bark smooth, gray; flowers white or purple; fruits erect, green, turning purplish or purple-red; seeds scarlet.

*Notes.* *Magnolia officinalis* resembles *Magnolia hypoleuca* in many characters except in the shape of the basal follicles of the ripe fruits, the degree of the indument of the pedicles, and the color of the twigs. In this regard, Spongberg (1976) has already compared the two species in detail; we agree with his observations. However, there are not sufficient collections available, particularly of living material, to settle the problem. Therefore, the two are treated as distinct species here.

This species was included as *Magnolia hypoleuca* auct. [non Siebold & Zucc. (1845)] by Diels (1900), Finet & Gagnepain (1905, pro parte), E. Wilson (1906) excluding description of the fruit., and Fang Wen Pei (1942).

9. **Magnolia rostrata** W. W. Smith., Notes Roy. Bot. Gard. Edinburgh 7: 213. 1920. TYPE: *Forrest 15052* (lectotype, selected here, E; isolectotype, K).

Deciduous tree to 24 m high; bark pale gray; twigs stout, 7–14 mm diam., yellow to purple-brown when dry, glabrous and smooth, covered with a gray waxy substance. Stipules glabrous, dull yellow-green, usually covered with waxy substance, adnate to the base of the petiole, stipular scars 1.5–3.5 cm long. Leaves thinly coriaceous, green, glossy and glabrous above, glaucous, sparsely scattered-pubescent with rather long, crisped, brown hairs, glabrescent beneath, 5–7 crowded together at the end of the twigs, obovate, 31–36.5(–53) × 19–20.5(–28) cm; apex broadly rounded, with a ca. 3-mm-long short-acute tip, base obtuse; midrib conspicuously elevated beneath, nerves prominent beneath, in 28–36 pairs, reticulation coarsely netted, visible on both sides. Petiole stout, pubescent, glabrescent, 2.5–6 cm long. Peduncles ca. 2.5 × 1 cm, pedicles ca. 1.3 cm long. Flowers appearing after the leaves, heavily scented; tepals 10–11, the outer 3 green, slightly flushed with pink outside, pink inside, oblong-elliptic, 8–13 × 2.5–5.6 cm, reflexed, the inner tepals 6, white, erect, spathulate to obovate, 11–13 × 4–4.5 cm; stamens purple-red, 1.4–1.7 cm long, anthers dehiscing introrsely, connective appendage triangular, 1–1.5 mm long, filaments 4–5 mm long; gynoecium cylindric, glabrous, 2.3–4 × 1–1.3 cm, carpels many; torus with the scars of perianth and stamens 1.2–1.9 × 0.6–1 cm. Fruiting peduncles 1.5–3.5 × 1–1.7 cm, pedicles 2–10 × 8 mm, sometimes absent, both glabrous. Fruits cylindric, erect, 12–20.5 × 3–5 cm, apex gradually narrowing, base broadly rounded; ripe carpels 1–1.5 cm long in the lower and 0.7–1.2 cm long in upper carpels, beak to 6–8 mm long, incurved. Seeds irregularly shaped, flat, ca. 7 × 5 mm.

*Distribution.* Northeastern Burma and China. In CHINA. **Xizang**: Mt. Kenichunpo, Upper Salween River, *Rock J.F. 22607*; Salween ridge, Champutong, *10160*; Mt. Kenyichunpo, Champutong, *11215*; Tsarong, *Forrest G. 20827*. **Yunnan**: Mount Gitsa, *Rock J.F. 17097, 18394*; N Waikha-Salwin divide, 26°30′N, *Forrest G. 18246*; Salween-Kui Chiang divide, 27°N, 98°35′E, *Forrest G. 25751*; Taron-Taru divide, Ahtemai, *Yu T.T. 20894*.

*Ecology.* In broad-leaved forest. Altitude: 2,400–2,800 m. Flowering April–May; fruiting September–October.

*Collector's note.* Leaves very large; flowers sweet-smelling, tepals 10–12, thick and fleshy, white, ivory, to white flushed rose or rose-pink, appearing before the foliage.

*Note.* The description of the flowers in Smith (1920) does not apply to this species.

**Ia-3. Magnolia** section **Oyama** Nakai, Fl. Sylv. Koreana 20: 117. 1933. *Magnolia* sect. *Cophantera* Dandy, Curtis Bot. Mag. 159: sub. t. 9467. 1936. TYPE: *Magnolia sieboldii* K. Koch.

Deciduous shrub or tree. Stipules adnate to petiole. Leaves ± pale green or glaucous, evenly distributed; midrib not prominent above. Flowers bisexual; tepals subequal; connective not produced into an appendage, retuse or blunt; anthers dehiscing introrsely. Gynoecium not stipitate. Scars of bracts 1. Fruits at least finally consisting of free follicles, which dehisce along the dorsal suture.

KEY TO THE SPECIES OF *MAGNOLIA* SECTION *OYAMA*

1. Leaves not glaucous beneath; pedicles 13–17 mm; nerves in 9–12 pairs; gynoecium 15–20 mm high. ..... 12. *Magnolia sinensis*
1. Leaves glaucous beneath. ..... 2
2(1). Gynoecium 23–25 mm high; nerves in 8–11 pairs; pedicles 5–25 mm. 10. *Magnolia globosa*
2. Gynoecium 13–20 mm high. ..... 3
3(2). Reticulation rather obscure; nerves in 6–8 pairs; pedicle 2–2.8 mm. 11. *Magnolia sieboldii*
3. Reticulation distinct; nerves in 10–12 pairs; pedicle 5–7 mm. ..... 13. *Magnolia wilsonii*

10. **Magnolia globosa** Hook. f. & Thomson, Fl. Ind. 1: 77. 1855. TYPE: Sikkim, alt. 2,700–3,000 m, *J. D. Hook. s.n.* (holotype, K; isotype, GH).

*Magnolia tsarongensis* W. W. Smith & Forrest, Notes Roy. Bot. Gard. Edinburgh 12: 215. 1920. TYPE: *G. Forrest 18870* (lectotype, selected here, A; isolectotypes, E, K).

Deciduous small tree to 10 m high, flowers appearing at the same time or before the leaves; young twigs purple-brown or dull brown, 4–5 mm diam., at first densely appressed or shaggily hairy with yellowish, brown to rusty-brown hairs, soon glabrous; terminal winter buds densely brown pubescent. Stipules yellowish sericeous or brown villous, adnate to higher on the petiole, stipular scars usually over half the length of the petiole, 15–42 mm long. Leaves membranous, dark green, usually dull brown when dry, sparsely pubescent along the midrib and nerves above, glaucous, villous with long, undulate to crisped, colorless or brownish hairs, later glabrescent beneath, ovate, broadly ovate, elliptic, occasionally obovate, 12.5–21(–26) × 6–11.5(–15) cm; apex acute to rounded, base rounded to somewhat cordate or truncate; midrib and nerves prominent beneath, nerves in 8–11 pairs, reticulation coarse, visible below. Petiole densely pubescent, glabrescent, 2–5 cm long. Flowers fragrant, cup-shaped to subglobose, pendent or nodding, 6–7.5 cm diam., peduncles densely villous with gray, brown, or rusty-brown hairs, 3.7–6.5(–7.5) × 0.2–0.4 cm, pedicles 5–25 mm long; tepals 9–12, creamy white, subequal, obovate to spathulate, 4–7.5 × 2–4 cm, apex rounded, base obtuse, usually constricted into short claws; stamens crimson, 12–18 mm long, anthers dehiscing introrsely, connective retuse or rounded, filaments 1–4 mm long; gynoecium green, ellipsoid, 2.3–2.5 × 0.5–0.8 cm. Fruiting peduncles 6.5–9 × 0.3–0.5 cm, glabrous or hairy. Fruits cylindric, 2.5–9 × 2–2.5 cm; ripe carpels 1.7–3 cm long in the lower and 1–2 cm long in the upper carpels, apically with beaks 3–6 mm long; scars of perianth and stamens along the torus 6–12 × 7–11 mm. Seeds ovoid, ca. 10 × 8 mm.

*Distribution.* Northeastern Assam, eastern Himalaya, China, northern Burma. In CHINA. **Southwestern Sichuan**: Wen Chaun Hsien, *Wilson E.H. 1422*. **Southeastern Xizang**: Mountains of Champutong, *Rock J.F. 22047*; Putsang River, Rong To valley, Zayul, *Kingdon Ward F. 10973*. **Northwestern Yunnan**: Salween-Kui Chiang divide, 23°24′N, 98°28′E, *Forrest G. 20866*; Salwin-Kiu Chiang divide, Si chi to, 28°45′N, 98°18′E, *21722*; Tsarong, Salwin-Kui Chiang divide 28°24′N, 98°24′E, *20303*; Meng-hua, Chukai, *Yu T.T. 15854*; Salween-Djiou-Djiang, under Tschamputong, *Hand.-Mazz. 9212*; Salwin-Kiukiang divide, *Yu T.T. 19251*; Sikang, *Li M.K. 2329*; Sitiping, between Lipiang and Weihsi, *Ching R.C. 22016*; Wei si Hsien, *Wang C.W. 63981*; Xue long Shan, *Feng K.M. 4813*.

*Ecology.* In mixed forest or thickets. Altitude: 1,900–3,300 m. Flowering May–July; fruiting August–September.

*Uses.* Seeds and leaves used for volatile oil, tree cultivated as an ornamental.

*Collector's notes.* With brown hairs on bracts, petioles, and under leaves; flowers snow white, creamy white, or greenish white, pendent and fragrant; fruits greenish, fleshy; seeds red.

*Note.* *Yulania japonica* Spach var. *globosa* (Hook. f. & Thomson) P. Parmentier (1895) is a nomen nudum.

11. **Magnolia sieboldii** K. Koch, Hort. Dendrol.: 4. 1853. *Magnolia oyama* Kort, Revue Horticulture Belge 31: 258. 1905. *Magnolia verecunda* Koidz., Bot. Mag. (Tokyo) 40: 339. 1926. SYNTYPES: *K. Ito s.n. L 908-126-1110*, fertile (L), sine leg. *L-908-126-1043* (L).

Deciduous treelet to 10 m high; young twigs slender, 1–2 mm diam., yellow-brown, dark brown, or purple-brown, at first densely appressed-pubescent with yellowish white hairs, later glabrous, smooth. Stipules sparsely to densely hairy with gray-yellow or brownish hairs, adnate to the petiole, scars up to over or under halfway on the petiole, 5–40 mm long. Leaves chartaceous, dark bright green, glabrous to sparsely pubescent with fine hairs above, glaucous, sparsely to densely covered with appressed short or long, colorless or brownish, usually straight to rarely undulate hairs beneath; obovate or broadly obovate, 3–15(–20) × 2–9(–12) cm; apex acute to acuminate with acumen 5–10 mm long, base rounded to truncate; midrib and nerves prominent below, nerves in 6–8 pairs, reticulation coarse, obscured. Petiole appressed-hairy, 1–4(–6.5) cm long. Flowers together with the leaves, cup-shaped to saucer-shaped, nodding or pendent, fragrant, 7–10 cm diam.; peduncles slender, densely hairy with gray-white or brownish hairs, 3.8–4.5 × 0.1–0.2 cm, pedicles 2–2.8 mm long, sometimes absent; tepals 9–12, white, subequal, 3.5–6 × 2–3.5 cm, the outer 3 obovate, reflexed in full bloom, the inner tepals 6, spathulate to broadly obovate, usually with short claw at the bases; stamens purple-red, 8–15 mm long, anthers dehiscing introrsely, connective blunt, ca. 0.5 mm long, filaments ca. 3 mm long; gynoecium green, ellipsoid, 1.5–1.7 × 0.4–0.6 cm; carpels narrowly

elliptic, ca. 1 cm long. Fruiting peduncles glabrous to densely brownish pubescent, 6.2–7 × 0.2–0.3 cm. Fruits cylindric, rarely ovoid, 3–4 × 1.2–1.7 cm; ripe carpels apically with 4–12-mm-long beaks, erect or recurved; torus with scars of perianth and stamens 4–10 × 3–5 mm. Seeds subcordate to irregularly shaped, ca. 6–7 × 6 mm.

*Distribution.* China, Korea, and Japan. In CHINA. **Anhui**: San Hua Wu, Huangshan, *Deng & Yao 79192.* **Northern Guangxi**: Quan Xian, *Chun Y.F. 81654*; Xing An, *Chen Z.Z. 51165*; Zi Yuan, *Tsoong C.H. 83515.* **Guizhou**: Lei Gong Shan, *Cao Zi-yu 369*; Lei Shan Xian, *Jian Z.P. 50796.* **Liaoning**: Huan Ren Xian, *Wang W.1191, Wang C.S. 4065.* **Sichuan**: Ma-pien Hsien, *Wang F.T. 22816*; Wenchuan Hsien, *Wang F.T. 21080.* **?Yunnan**: *Wang C.W. 89858.*

*Ecology.* In forest. Altitude 1,500–1,800 m. Flowering May–June; fruiting August–September.

*Uses.* Used for medicinal purposes; grown as an ornamental.

*Collector's notes.* Small tree or shrub; flowers nodding, white and fragrant; stamens creamy white, with rose tip.

*Notes.* Siebold & Zuccarini (1845) treated this species as *Magnolia parviflora* [non Blume (1825)], while Komarov (1904) used the name *Magnolia conspicua* [non Salisbury (1806)].

12. **Magnolia sinensis** (Rehder & E. H. Wilson) Stapf, Bot. Mag. (Curtis) 149: t. 9004. 1924. *Magnolia globosa* Hook. f. & Thomson var. *sinensis* Rehder & E. H. Wilson in Sarg., Pl. Wilson. 1: 393. 1913. *Magnolia sieboldii* K. Koch subsp. *sinensis* (Rehder & E. H. Wilson) Spongberg, J. Arnold Arbor. 57: 279, f. 3, h–i. 1976. TYPE: *E. H. Wilson 1422* (holotype, A; isotypes, E, GH, US).

Deciduous shrub or small tree to 5 m high; young twigs purple-brown, dark purple, purple-gray to gray, slender, ca. 3 mm diam., densely yellow or brownish villous at first, glabrescent later, old twigs brown-gray, smooth, glabrous to barely hairy. Stipules densely appressed-pubescent with brownish or yellowish hairs, adnate to the petiole, scars 2–3 cm long. Leaves chartaceous, green, finely pubescent over the surface or only along midrib and nerves above, pale green, at first densely covered with rather long, crisped, colorless or brownish hairs, soon glabrescent beneath, elliptic, broadly elliptic, obovate to broadly obovate, 10–16(–21.5) × 6–9(–13) cm; apex rounded or mucronate, base obtuse; nerves visible below, in 9–12 pairs, reticulation coarse. Petiole densely yellowish villous, 2.5–4(–7) cm long. Flowers appearing with the leaves, nodding, fragrant, cup-shaped, 8–12(–15) cm diam. when fully open; peduncles densely or sparsely pubescent, 3.5–6.5 × 0.2–0.5 cm, pedicles 1.3–1.7 cm long; tepals 9, white, subequal, the outer 3 ovate to elliptic, 4–5.5 × 1.7–2.7 cm, the inner tepals 6, broadly obovate, with short claw at the bases, 4.5–7 × 3–5.6 cm; stamens red, 9–14 mm long, anthers dehiscing introrsely, connective rounded to mucronulate, ca. 0.5 mm long, filaments 1–2 mm long; gynoecium green, narrowly obovoid-ellipsoid, 1.5–2 × 0.4–0.7 cm, carpels narrow and long, styles 3–4 mm long. Fruiting peduncles 4–6.5 × 0.2–0.5 cm. Fruits cylindric, 5.5–7.5 × 1.3–1.7 cm; ripe carpels ellipsoid, 1.7–2.5 cm long in the lower and 1–1.3 cm in the upper carpels, beaks 2–5 mm long, recurved; torus with scars of perianth and stamens 8–10 × 4–9 mm.

*Distribution.* CHINA: northwestern **Sichuan**.

*Uses.* The tree is used as an ornamaental.

*Note.* There is still disagreement about the rank of this species. Ueda's (1980) observation and judgment dealing with this species seem accurate. We agree with his view that *Magnolia sinensis* should not be treated as a subspecies of *Magnolia sieboldii.*

13. **Magnolia wilsonii** (Finet & Gagnep.) Rehder in Sarg. Pl. Wilson. 1: 395: 1913. *Magnolia parviflora* var. *wilsonii* Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 39. 1905. TYPE: *E. H. Wilson 3137* (holotype, A; isotypes, BM, K, US).

*Magnolia nicholsoniana* Rehder & E. H. Wilson in Sarg. Pl. Wilson. 1: 394. 1913. *Magnolia wilsonii* f. *nicholsoniana* (Rehder & E. H. Wilson) Rehder, J. Arnold Arbor. 20: 91. 1939. TYPE: *E. H. Wilson 838* (holotype, A; isotypes, BM, K, US).

*Magnolia taliensis* W. W. Smith, Notes Roy. Bot. Gard. Edinburgh 8: 341. 1915. *Magnolia lilifera* var. *taliensis* (W. W. Smith) Pamp., Bull. Soc. Tosc. Ortic. 41: 137. 1916. *Magnolia wilsonii* f. *taliensis* (W. W. Smith) Rehder, Man. Cult. Trees: 249. 1940. TYPE: *G. Forrest 7182* (holotype, E; isotypes, BM, K).

Deciduous shrub or small tree to 8 m high; bark gray-brown; young twigs slender, 2–3 mm diam., brown-purple to gray, densely villous with yellowish to brown hairs, later glabrescent, smooth and sparsely lenticellate, old twigs gray-black, glabrous, glabrescent. Stipules densely yellow to yellowish white villous with silky hairs, adnate to the petiole, stipular scars nearly up to the base of the blade, 1–2.5(–5.4) cm long. Leaves chartaceous, dark

green, glabrous or sparsely pubescent over the surfaces to only hairy along both midrib and nerves above; glaucous, glabrous, sometimes only pubescent along midrib and nerves, or thinly to densely pubescent with short to long, colorless to brownish, straight, slightly curved to rather crisped hairs everywhere beneath; usually narrowly ovate to obovate, sometimes broadly ovate to elliptic, 9–14.5(–22) × 3.5–6(–10) cm; apex acute or acuminate, base rounded or sometimes slightly cordate; midrib and nerves visible on both sides, nerves in 10–12 pairs, reticulation coarse. Petiole slender, densely covered with same indumentum as young twigs, soon glabrescent, 2–4(–5.6) cm long. Flowers appearing with the leaves, at first cup-shaped to saucer-shaped, later pendent, white, fragrant; peduncles slender, brown-villous with silky hairs, glabrescent, 13–45 × 2–3 mm, pedicles 5–7 mm long; bracts pubescent; tepals 9(–12), subsimilar, the outer 3 elliptic, apically rounded to acute, 4.5–6 × 1.5–3 cm, the inner tepals 6, broadly obovate to spathulate, apically rounded, basally short-clawed, 2.7–6.5 × 1.3–4.5 cm; stamens 9–12 mm long, purple-red, connective rounded, filaments ca. 2 mm long; gynoecium green, ovoid-cylindric, 13–20 × 5–6 mm; torus with the scars of perianth and stamens ca. 6 × 6 mm. Fruiting peduncles glabrous, 30–45 × 2–3 mm, pedicles 8–15 mm long. Fruits pendent, cylindric, 3–6.5 × 1–2 cm; ripe carpels ellipsoid, 1.7–2.6 cm long in the lower and 1–2 cm long in the upper carpels, with beaks 2–5 mm long. Seeds subcordate to irregularly shaped, 5–7 × 5–6 mm.

*Distribution.* CHINA. **Guizhou**: Xing Yi Xian, *An Shun Exped. 1112.* **Western & central Sichuan**: Naitan to pain yi pu, *Smith, Harry 1953*; Tachinhu, *Wilson E.H. 1374*; Wa shan, *838.* **Yunnan**: Tze-tchou-pa, *Maire E.E. 866*; Tali range, 25°40′N, 100°5′E, *Forrest G. 27941*; Yun Hsien, *McLarens's collectors L 66 A*; Liao Tseng, *C 92*; Kou ty, Pe yen tsin, *Ten Simeon 564*; Chienchuan–Mekong divide, *Forrest G. 23480*; N end of Cangshan, *Sino-British Exped. 655.*

*Ecology.* In forest. Altitude: 1,900–3,300 m. Flowering May–June, fruiting September–October.

*Uses.* Bark used for medicinal purposes; the tree is grown as an ornamental.

*Collector's notes.* Flowers saucer-shaped, drooping, fragrant, pure white; stamens bright red or violet.

*Note.* E. Wilson (1906) dealt with this species erroneously under *Magnolia globosa* Hook. f. & Thomson.

**Ia-4. Magnolia** section **Gynopodium** Dandy, Curtis Bot. Mag. 155: t. 16. 1948. TYPE SPECIES: *Magnolia nitida* W. W. Smith.

*Parakmeria* Hu & Cheng, Acta Phytotax. Sinica 1, 2: 1. 1951. TYPE SPECIES: *Parakmeria omeiensis* Hu & Cheng.

*Micheliopsis* H. Keng, Quart. J. Taiwan Mus. 8: 207, t. 345. 1955. TYPE SPECIES: *Micheliopsis kachirachirai* (Kaneh. & Yamam.) H. Keng.

Evergreen tree, entirely glabrous. Stipules free. Leaves evenly distributed. Midrib prominent above, at least toward base, or not. Flowers androdioecious. Tepals subequal. Connective produced into a short or long appendage. Anthers dehiscing introrsely. Gynoecium stipitate. Number of ovules per carpel 2, sometimes 4 in the lower carpels (rarely 4 in each carpel). Fruits at least finally consisting of free follicles, which dehisce along the dorsal suture.

KEY TO THE SPECIES OF *MAGNOLIA* SECTION *GYNOPODIUM*

1. Outer tepals 3.1–5 cm long. ..... 2
1. Outer tepals 2.5–3 cm long. ..... 4
2(1). Midrib of leaf prominent above, at least toward base; leaves ovate, base broadly cuneate or rounded; filaments 1–3 mm, connective appendage of anthers 2–4 mm. ..... 15a. *Magnolia nitida* var. *nitida*
2. Midrib of leaf not prominent above; leaves elliptic, obovate, or narrowly elliptic, base cuneate or narrowly cuneate; filaments 2–2.5 or 7 mm; connective appendage of anthers 1–1.5 mm. ..... 3
3(2). Peduncle 6 mm thick; leaves narrowly elliptic, base narrowly cuneate; flower creamy white, outer tepals thin, oblong; filaments 7 mm. ..... 16. *Magnolia omeiensis*
3. Peduncle 3–4 mm thick; leaves elliptic or obovate, base cuneate; flower yellowish green, tepals subsimilar, obovate or spathulate; filaments 2–2.5 mm. .. 14. *Magnolia kachirachirai*
4(1). Peduncle 3–4 mm thick; midrib of leaf not prominent above; outer tepals obovate or spathulate; filaments 2–2.5 mm long; gynoecium exserted from stamens; fruits 2–2.5 cm long. ..... 14. *Magnolia kachirachirai*
4. Peduncle 5–9 mm thick; midrib of leaf prominent above, at least toward base; outer tepals ovate, filaments 1 mm long; gynoecium entirely hidden within androecium, fruits 3.5–7.5 cm long. ..... 5
5(4). Gynoecium 8 mm high; reticulation of leaf distinct; connective appendage of anthers 0.5 mm long; gynoecium narrowly ovoid; scars of perianth and stamens along torus under fruit 6–7 mm long. ..... 15c. *Magnolia nitida* var. *robusta*
5. Gynoecium 16 mm high; reticulation rather obscure, connective appendage 2–4 mm long;

gynoecium ovoid, scars of perianth and stamens along torus under fruit 2–4 mm long. ..... 15b. *Magnolia nitida* var. *lotungensis*

14. **Magnolia kachirachirai** (Kanehira & Yamamoto) Dandy, Kew Bull. 1927: 264. 1927. *Michelia kachirachirai* Kanehira & Yamamoto, Trans. Nat. Hist. Soc. Taiwan 84: 78. 1926. *Micheliopsis kachirachirai* Keng, Quart. J. Taiwan Mus. 8: 210, pl. 1 and f. 1. 1955. *Parakmeria kachirachirai* Law in W. C. Cheng, Sylva Sinica 1: 473. 1983. TYPE: *Kanehira*, 1924 (holotype, TAIF not seen).

Evergreen glabrous tree to 17 m high and 1.2 m diam., bark dark brown, smooth, young twigs 2–3 mm diam., dull dark brown, smooth, old ones gray, longitudinally fissured; terminal buds ovoid to elliptic, dull brown, 13–16 × 3–4 mm. Stipules free from the petiole. Leaves thinly coriaceous, dark green above, green beneath, elliptic to obovate, 6.5–12(–20) × 2–3(–5) cm; apex acute to short-acuminate, base cuneate; nerves fine, obscured above, visible below, in 9–12 pairs, reticulation rather coarse, faint on both sides. Petiole ca. 5–20 mm long. Peduncles 7–15 × 3–4 mm, pedicles usually absent, rarely present, ca. 1 mm long. The bisexual flowers yellowish green; tepals 9–12, subsimilar, obovate to spathulate, 2.5–4 × 1–1.5 cm; stamens 50–60, 1.4–1.8 cm long, anthers dehiscing introrsely, connective appendage narrowly triangular, ca. 1 mm long, filaments 2–2.5 mm long; gynoecium ovoid, slightly exserted from the androecium, 1.2–1.4 × 0.5 cm long, gynophore ca. 5–8 × 1.5 mm, carpels 10–18; torus with the scars of perianth and stamens ca. 5 × 4 mm; the male flowers not seen. Fruits subovoid, 2–2.5 × 1.2–1.5 cm; ripe carpels 8–12, ± connate, 2–2.5 cm long. Seeds reniform to subcordate, ca. 10 × 7 mm.

*Distribution.* CHINA. **Southeastern Taiwan**: Hengchun peninsula, *Henry A 2060, Chang C.E. 4384*; Taizhong, *Xie Z.Q. s.n.*

*Ecology.* In evergreen broad-leaved forest. Altitude: 500–1,300 m.

*Uses.* Wood used for general construction work; tree also grown as an ornamental.

15. **Magnolia nitida** W. W. Smith, Notes Roy. Bot. Gard. Edinburgh 12: 212. 1920. *Parakmeria nitida* (W. W. Smith) Law in W. C. Cheng, Sylva Sinica 1: 472. 1983. TYPE: *Forrest 15059* (lectotype, selected here, E; isolectotype, K).

*Magnolia lotungensis* Chun & C. T. Tsoong, Acta Phytotax. Sin. 8: 285. 1963. TYPE: *Chun & Tao 50122* (IBSC not seen).

*Magnolia yunnanensis* (Hu) Noot., Blumea 31, 1: 88. 1985. *Parakmeria yunnanensis* Hu, Acta Phytotax. Sin. 1: 2. 1951. TYPE: *C. W. Wang 83157* (KUN).

15a. **Magnolia nitida** var. **nitida**

Evergreen tree to 30 m high and 90 cm diam., entirely glabrous, bark faintly gray-brown or dark gray; young twigs 2–3 mm diam., olive green to brownish, fruiting twigs 5–6(–8) mm diam., old ones dull gray, longitudinally to irregularly fissured; terminal buds ovoid, ca. 17 × 5 mm. Stipules free from the petiole. Leaves rigid, coriaceous, dark glossy green, olive green to dull brown when dry above, green, greenish brownish to brownish when dry beneath, usually ovate to elliptic-ovate, occasionally obovate, 6–12(–14) × 3–4(–6.5) cm; apex short-acuminate, acumen 7–10 mm long, sometimes acute, base broadly cuneate to obtuse; midrib prominent above only near the base; nerves fine, visible on the underside, in 9–13 pairs, reticulation coarse, hardly visible on both surfaces. Petiole 1.5–2.5 cm long, without stipular scars. The bisexual flowers fragrant, peduncles 6–8 × 5 mm, pedicles 1.5–2 mm long; tepals 9–12, subsimilar, creamy yellow, slightly fleshy, flushed purplish outside, obovate to spathulate, 4–5 × 1–3 cm; apex rounded to short-acuminate, base tapering, sometimes short-clawed; stamens 1.3–2.5 cm long, anthers dehiscing introrsely, connective appendage linear, 2–4 mm long, filaments 1–3 mm long; gynoecium oblong, exserted from the androecium, ca. 16 × 5 mm, gynophore 6–8 × 2–3 mm; carpels green, styles crimson; the male flowers not seen. Fruiting peduncles 8–16 × 4–5 mm, pedicles 1.5–4 mm long. Fruits ovoid to oblong, sometimes distorted, 3.5–7.5 × 2–3 cm; ripe carpels 13–20, 1–2.5 cm long, apically with recurved beaks ca. 1 mm long, gynophores 4–12 × 4–6 mm; scars of perianth and stamens along the torus 5–10 × 4–7 mm. Seeds reniform, 10–13 × 5–10 mm.

*Distribution.* China and northern Burma. In CHINA. **Xizang**: Champutong, *Rock J.F. 10136*; Mt. Kenichunpo, W of Champutong, *Rock J.F. 22457*; Salween valley, Champutong, *10235*; Tsarong, *G. Forrest 20358.* **Yunnan**: Salwin-Kiu Chan divide, Champutong, 98°30′E, 28°16′N, *Forrest G. 21616*; Salwin-Kiu Chang divide, 28°24′N, 98°24′E, *20860*; Shweli-Salwin divide, 25°50′N, 98°45′E, *26381*; Meng Lun, *Chang H.T. 5022*; Shang pa Hsien, *Tsai H.T. 54858.*

*Ecology.* In mixed forest, growing on sandstone, shale, and granite. Altitude: 800–2,500 m. Flowering March–May; fruiting September–October.

*Uses.* Wood yellowish, durable, generally used for construction work and furniture.

*Collector's notes.* Widely branched evergreen tree, or half deciduous; leaves whitish beneath; flowers fragrant, creamy white, pale yellow or white washed purple toward base; fruits green.

*Notes.* This species is widely distributed, extending from northern Burma northward to Xizang and northern Yunnan, and northeastward to central and southeastern Yunnan. *Magnolia yunnanensis* is very similar to *Magnolia nitida* in all characters. It is obvious that the leaves, the mature fruits, the peduncles, and the gynophores become increasingly longer along a cline from Burma to southeastern Yunnan. No characters can be found that segregate *Magnolia nitida* from *Magnolia yunnanensis.*

15b. **Magnolia nitida** var. **lotungensis** (Chun & C. T. Tsoong) B. L. Chen & Nooteboom, stat. nov. *Magnolia lotungensis* Chun & C. T. Tsoong, Acta Phytotax. Sin. 8: 285. 1963. TYPE: *Chun & Tao 50122* (IBSC not seen).

Evergreen tree to 20 m high and 90 cm diam., bark pale gray to brownish gray; young twigs 2–3 mm diam., dull brown-green, fruiting twigs 4–5(–6) mm diam., old ones faint gray; terminal buds ovoid-ellipsoid, ca. 14 × 4 mm. Leaves coriaceous, dark green, shiny, olive green to dull brown when dry above, green, brownish when dry beneath, rigid, elliptic to narrowly elliptic, occasionally broadly elliptic, 6–11 × 2.5–3.5(–5) cm; apex acute to short-acuminate, base cuneate; midrib prominent on both sides, nerves fine, hardly visible above, prominent below, in 9–13 pairs, reticulation coarsely netted, obscured on both surfaces. Petiole ca. 1.5–2 cm long, without stipular scars. Flowers androdioecious, white; tepals 9–12, subsimilar, the outer 3 ovate, 2.5–3 × 1.2–2 cm, the inner tepals 6–9, obovate, slightly narrower than the outer; stamens 35–65, anthers 9–10 mm long, filaments ca. 1 mm long in the male flowers; stamens 17–22, gynoecium ovoid, entirely hidden by the androecium, carpels 15–20 or much less in the bisexual flowers. Fruiting peduncles 4–9 × 4–7 mm, pedicles absent. Fruits obovoid to ovoid-oblong, 3.5–4.5 × 2.5–3 cm; gynophore 1–5 × 5–6 mm; ripe carpels 10–13, rarely 1–4, ± connate, 1.8–2.2 cm long; scars of perianth and stamens along the torus 2–4 × 5–6 mm. Seeds ellipsoid to ovoid, 7–12 × 6–7 mm.

*Distribution.* CHINA. **Guangdong**: Ruyuan, *Ko S.P. 53691, Guangdong Mucai Yanjiu Zu 32*; Yangchung, *Liu J.H. 89847.* **Guangxi**: Da Miao Shan, *Lu Q.H. 2873*; Jia Xian, *Wang C. 40158*; Jin Xiu Xian, *Da Yao Shan Exped. 13429*; Da Ming Shan, *Cai C.X. 5470*; Lin Gui, *Deng X.F. 231*; Long Sheng, *Long Sheng Exped. 130.* **Guizhou**: Li Ping Xian, *Yuan J.M. 332.* **Hainan**: Dong Fang Xian, *Chen Y.W. 7620*; Fan Yah, *Chun N.K. & C.L. Tso 44041*; Loktung, *Lau S.K. 27375.* **Hunan**: Mang Shan, *Li B.G. et al. 59*; Xin Ning, *Liu L.Y. 15146.* **Zhejiang**: Tai Suan, *Ching R.C. 2167.*

*Ecology.* In forest. Altitude: 800–1,100 m. Flowering April; fruiting September–October.

*Uses.* Wood used for general construction work and furniture.

*Note.* This variety is so similar to *Magnolia nitida* that we do not distinguish them easily. In general, variety *lotungensis* has elliptic to narrowly elliptic leaves, fewer carpels, and the gynoecium is hidden by the androecium. Unfortunately, sufficient flowers of *Magnolia nitida* var. *lotungensis* were not available for comparison to be made.

15c. **Magnolia nitida** var. **robusta** B. L. Chen & Nooteboom, var. nov. TYPE: China. Annam, Massif de Bi-doup, 17 Oct. 1940, alt. 2,000 m, *Poilane 31039* (holotype, P; isotype, L). Figure 1.

A var. nitida differt ramulis crassioribus sub fructibus foliis grandioribus petiolis longioribus.

Tree 25–30 m high, ca. 1 m diam., glabrous; young twigs ca. 3 mm diam., fruiting ones stout, ca. 8 mm diam., dull olive-brown, old ones quite rough, longitudinally and transversely irregularly fissured; terminal buds ovoid to ovoid-ellipsoid, ca. 15 × 5 mm. Stipules free from the petiole. Leaves coriaceous, rigid, green, slightly glossy above, greenish beneath, ovate-elliptic to ovate, 7–16.5 × 3.5–6.5 cm; apex acute to acuminate or obtuse, base cuneate; midrib slightly prominent above, conspicuously elevated below, nerves visible on both sides, in 12–15 pairs, reticulation coarse, prominent on both sides. Petiole ± flat, dilatate toward the base, 1.6–4.7 cm long. In the male flower, peduncle 10–13 × 6–7 mm, pedicle absent; tepals not seen; scars of perianth and stamens ca. 10 × 6 mm. In the bisexual flower, peduncle ca. 5.2 × 9 mm, pedicle ca. 2 mm long; bracts 2, 2.2–3 cm long; tepals 9, the outer 3 much larger than the inner ones, the former ovate, ca. 2.5 × 1.5 cm, the latter 6, 2.2–2.5 × 1.2 cm, spathulate, obovate to narrowly obovate, tapering toward the

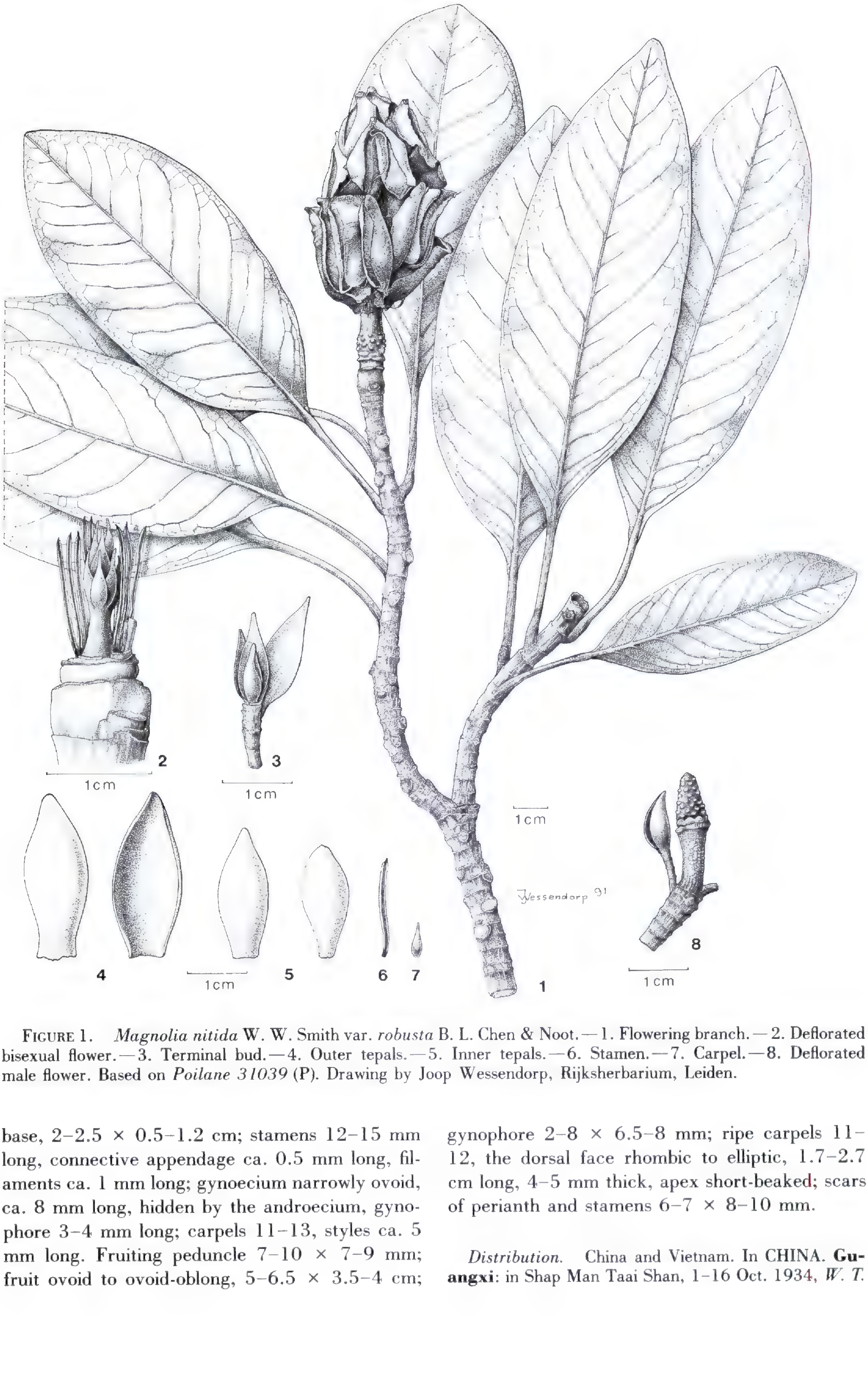


FIGURE 1. *Magnolia nitida* W. W. Smith var. *robusta* B. L. Chen & Noot.—1. Flowering branch.—2. Deflorated bisexual flower.—3. Terminal bud.—4. Outer tepals.—5. Inner tepals.—6. Stamen.—7. Carpel.—8. Deflorated male flower. Based on *Poilane 31039* (P). Drawing by Joop Wessendorp, Rijksherbarium, Leiden.

base, 2–2.5 × 0.5–1.2 cm; stamens 12–15 mm long, connective appendage ca. 0.5 mm long, filaments ca. 1 mm long; gynoecium narrowly ovoid, ca. 8 mm long, hidden by the androecium, gynophore 3–4 mm long; carpels 11–13, styles ca. 5 mm long. Fruiting peduncle 7–10 × 7–9 mm; fruit ovoid to ovoid-oblong, 5–6.5 × 3.5–4 cm; gynophore 2–8 × 6.5–8 mm; ripe carpels 11–12, the dorsal face rhombic to elliptic, 1.7–2.7 cm long, 4–5 mm thick, apex short-beaked; scars of perianth and stamens 6–7 × 8–10 mm.

*Distribution.* China and Vietnam. In CHINA. **Guangxi**: in Shap Man Taai Shan, 1–16 Oct. 1934, *W. T.*

*Tsang 24463*. VIETNAM. **Annam**: massif de Bi-doup, 23 Nov. 1914, alt. 2,000 m, *Poilane 31039* (TYPE); Binh Tri Thiên, 7 Oct. 1949, alt. 1,500 m, *J. E. Vidal 1034A*.

*Collector's note*. In rocky thicket, woody; flower yellow, fragrant.

*Note*. This variety is characterized by stout twigs, especially the fruiting twigs, larger leaves, longer petioles, whose length is usually less than 4 times that of the leaves, short peduncles, a few carpels, a thick wall of mature carpels, and the gynoecium hidden by the androecium instead of exceeding the androecium as in *Magnolia nitida* var. *nitida*. The specimen from Guangxi bearing smaller leaves, without any flowers or fruits, is here treated as this variety based on the shape of the leaves and the relative length of the blade and the petiole.

16. **Magnolia omeiensis** (Hu & Cheng) Dandy in Praglowski, World Pollen & Spore Fl. 3: 5. 1974. *Parakmeria omeiensis* Hu & Cheng, Acta Phytotax. Sin. 1(1): 2. 1951. TYPE: *W. C. Cheng 10525* (holotype, PE; isotype, A).

Tree to 20 m high and 40 cm diam., bark dark gray; plant entirely glabrous; twigs 2–2.5 mm diam., smooth, dull brown-black when dry. Stipules free from the petiole. Leaves coriaceous, dark green, shiny above, pale green beneath, narrowly elliptic, 7.5–12 × 2–4.5 cm; apex short-acuminate, sometimes acute, base narrowly cuneate; nerves fine, in 8–10 pairs, reticulation coarse, hardly visible on both sides. Petiole 1–2 cm long, without stipular scars. Peduncle ca. 10 × 6 mm, pedicle absent. Male flowers creamy white, tepals 12, the outer 3 thin, oblong, apex obtuse, ca. 3.8 × 1.3 cm, the inner tepals 6, spathulate to obovate, 3.5–4.2 × 1–1.5 cm; stamens crimson, 2–2.2 cm long, anthers dehiscing introrsely, connective appendage triangular, ca. 1.5 mm long, filaments ca. 7 mm long; torus ovate-orbicular, 4 mm long.

*Distribution*. CHINA. **Sichuan**: Emei Shan, *Cheng W.C. 10525, Chow H.C. 12095*.

*Ecology*. In evergreen broad-leaved forest. Altitude: 1,000–1,200 m.

*Note*. *Magnolia kachirachirai*, *Magnolia nitida*, and *Magnolia omeiensis*, which all belong to *Magnolia* sect. *Gynopodium*, can barely be distinguished by their vegetative characters; the knowledge of their flowers is still far from satisfactory. Unfortunately, we were unable to see enough material, especially collections with flowers. The delimitation of these species is obviously obscure. Until more material is available they are maintained as different species here.

**Ia-5. Magnolia** section **Alcimandra** (Dandy) Nooteboom, Blumea 31: 88. 1985. *Alcimandra* Dandy, Kew Bull. 1927: 260. 1927. TYPE SPECIES: *Magnolia cathcartii* (Hook. f. & Thomson) Noot.

Evergreen tree. Stipules free. Leaves evenly distributed; midrib not prominent above. Flowers bisexual; tepals subequal; connective produced into a short linguiform appendage; stamens with short filaments and long anthers, completely hiding the gynoecium; anthers dehiscing introrsely. Gynoecium stipitate. Number of ovules per carpel 2–5. Fruits at least finally consisting of free carpels, which dehisce along the dorsal suture.

17. **Magnolia cathcartii** (Hook. f. & Thomson) Nooteboom, Blumea 31: 88. 1985. *Michelia cathcartii* Hook. f. & Thomson, Fl. Ind. 1: 79. 1855. *Sampacca cathcartii* (Hook. f. & Thomson) Kuntze, Revis. Gen. Pl. 1: 6. 1891. *Alcimandra cathcartii* (Hook. f. & Thomson) Dandy, Kew Bull. 1927: 260. 1927. TYPE: Sikkim, *J. D. Hook. s.n.* (holotype, K; isotypes, A, GH, NY).

Tree to 25 m high and 50 cm diam.; young twigs dark brown, slender, 1–2 mm diam., densely appressed-pubescent with long, straight to ± undulate or curly, yellowish to gray hairs, old ones dull brown-gray, glabrescent, sparsely supplied with conspicuously elevated, elliptic to suborbiculate, white lenticels; terminal buds narrowly ovoid, covered with an indumentum as young twigs, 0.6–2.5 cm long. Stipules hairy, free from the petiole. Leaves coriaceous, dark green, shiny above, both sides glabrous, ovate to elliptic-ovate, occasionally obovate, 6.5–17 × 3–5.6 cm; apex long-acuminate, acumen 0.6–2 cm long, sometimes acute, base obtuse to broadly cuneate; midrib densely pubescent, glabrescent at both sides, nerves fine, prominently elevated on both surfaces, in 12–15 pairs, reticulation densely netted, visible on both sides when dry. Petiole pubescent, glabrescent above, 0.2–2 cm long, without stipular scars. Peduncles usually slender, rarely stout, ca. 15–20 × 2 mm, glabrous, pedicles 0–4 mm long; tepals 9, white, the outer 3 oblong, 5.5–6 × 2–2.5 cm, the inner tepals 6, obovate-elliptic, ca. 5.5 × 2.5 cm; stamens 3–4 cm long, anthers introrsely dehiscent, connective appendage tonguelike, ca. 2 mm long, filaments ca. 1 cm long; gynoecium stipitate, cylindric, ca. 2 cm long. Fruiting peduncles 15–35 × 2–4 mm. Fruits usually irregularly shaped, 3.5–6.5 × 1.5–2 cm; ripe carpels 3–16, compressed-subglobose, ca. 8–9 mm diam., white-lenticellate;

gynophore 5–8 × 2–4 mm; torus with the scars of perianth and stamens 4–7 × 4–5 mm. Seeds subellipsoid, ca. 8 × 7 mm.

*Distribution.* Sikkim, Assam, China, Upper Burma to Vietnam. In CHINA. **Southern & southeastern Xizang**: Yunnan, Jingdong Xian, *Xu S.G. 5024*; Kiukiang Valley, Muchietu, *Yu T.T. 21016*; Lan-Tsang Hsien, *Wang C.W. 76855*; Meng-soong, Dahmeng-lung, Che-li Hsien, *78440*; Shangpa, *Tsai H.T. 58698*; Wenshan, *Feng K.M. 22416.*

*Ecology.* In forest. Altitude: 1,800–2,800 m. Flowering May; fruiting August–October.

*Collector's notes.* In mixed woods; flowers yellow-green; fruits green, blue to brown-green; seeds black with orange-red fleshy coat.

**Ib. Magnolia** subgenus **Yulania** (Spach) Reichenbach, Der Deutscher Botaniker 1: 192. 1841. *Yulania* Spach, Hist. Natur. Veget., Phanerog. 7: 462. 1839. *Magnolia* subg. *Pleurochasma* Dandy, J. Roy. Hort. Soc. 75: 161. 1950. TYPE SPECIES: *Yulania conspicua* Spach = *Magnolia heptapeta* (Buchoz) Dandy.

Leaves evenly distributed, deciduous; midrib not prominent above. Flowers bisexual, precocious and/or with a much reduced calyxlike outer whorl of tepals; anthers dehiscing laterally or sublaterally, connective produced into a short or long appendage. Gynoecium not stipitate. Fruit cylindric or oblong, usually ± distorted, at least finally consisting of free carpels which dehisce along the dorsal suture.

**Ib-1. Magnolia** section **Yulania** (Spach) Dandy in Camellias and Magnolias Conf. Report: 72. 1950.

Flowers appearing before the leaves (or some late flowers with the leaves), pink, (greenish) white, purple, or red. Tepals subequal.

KEY TO THE SPECIES OF *MAGNOLIA* SECTION *YULANIA*

1. Gynoecium 8–15 mm high. ..... 2
1. Gynoecium 20–40 mm high. ..... 3
2(1). Twigs yellowish brown to black or gray-brown; leaves not glaucous beneath, reticulation coarse; flower purple or red; pedicle 12–15 × 5–6 mm. ..... 22. *Magnolia sargentiana*
2. Twigs yellowish green turning reddish brown; leaves glaucous beneath, reticulation fine; flower white; pedicle 7–12 × 3–4 mm. ..... 20. *Magnolia dawsoniana*
3(1). Flower purple or red. ..... 4
3. Flower pink or white. ..... 5
4(3). Tepals 7–8 cm long; stamens 15–17 mm long; leaf base broadly cuneate or rounded, apex short-acuminate; stipular scars 3–7 mm. ..... 24. *Magnolia zenii*
4. Tepals 5–6.5 cm long; stamens 9–10 mm long; leaf base cuneate, apex acuminate or acute; stipular scars 1–3 mm. ..... 18. *Magnolia amoena*
5(3). Peduncle 25–30 mm long; fruiting peduncles 2.7–5 cm long. ..... 19. *Magnolia campbellii*
5. Peduncle 10–20 mm long; fruiting peduncles 1–2 cm long. ..... 6
6(5). Twigs glabrous; tepals 12; terminal winter buds densely villous; reticulation of leaves distinct; flowers appearing together or after the leaves; filaments 5–7 mm long. 23. *Magnolia sprengeri*
6. Twigs finely appressed-pubescent; tepals 9; terminal winter buds sericeous; reticulation of leaves rather obscure; flowers appearing before the leaves; filaments 3–4 mm long. ..... 21. *Magnolia heptapeta*

18. **Magnolia amoena** W. C. Cheng, Contr. Biol. Lab. Sci. Soc. China Bot. Series 9: 280, f. 28. 1933. TYPE: *S. Chen 2692*, in flower (lectotype, selected here, PE; isolectotype, A).

Deciduous tree to 12 m high; bark gray or gray-white; young twigs 2–3 mm diam., slender, purple-brown, glabrous; terminal buds white sericeous with long hairs. Stipules adnate to the petiole, stipular scars 1–3 mm long. Leaves thinly coriaceous, glabrous above, curly hairy with long white hairs along the midrib, the nerves and at the junctions of the midrib and the nerves beneath, obovate to obovate-elliptic, 10–15 × 3.5–5 cm; apex acute to cuspidate with a ca. 15-mm-long tip; base cuneate, somewhat unequal; nerves in 10–13 pairs, nerves and reticulations prominent on both sides; petiole pubescent, 8–13 mm long. Flowers appearing before the leaves, fragrant, ca. 6 cm diam. Peduncles 6–8 × 4 mm, pedicles 3–4 × 4 mm, both densely yellowish to white hairy. Tepals 9, subsimilar, red to reddish, spathulate to oblanceolate, 5–6.5 cm long; stamens ca. 9–10 mm, connective appendage short-pointed, ca. 1 mm long, anthers dehiscing laterally, filaments purple, ca. 3 mm long; gynoecium cylindric, ca. 2 cm long, styles ca. 1 mm long. Fruits cylindric, 4–6 cm long, often curved as carpels partly abortive; fruiting peduncles long white pubescent, ca. 10 × 4 mm; ripe carpels oblong, apex rounded, papilliferous.

*Distribution.* CHINA. **Southern Anhui**: Huoshan, *Yin S.F. 14*. **Southern Jiangsu**: Zhejiang, W Tienmushan, *Cheng W.C. 4444 A.*

*Ecology.* In forests. Altitude: 700–1,000 m. Flowering April–May; fruiting September–October.

*Note.* The description was drawn from the type specimen only. There are no other collections available.

19. **Magnolia campbellii** Hook. f. & Thomson, Fl. Ind. 1: 77. 1855. TYPE: Sikkim, *J. D. Hook. & Thomson s.n.* (holotype, K; isotypes, GH, NY).

*Magnolia mollicomata* W. W. Smith, Notes. Roy. Bot. Gard. Edinburgh 12: 211. 1920. TYPE: *Forrest 14466* (lectotype, selected here, E).

Deciduous tree to 30 m high; bark gray-brown; young twigs usually purple-brown, sometimes brown to gray-green when dry, 4–7 mm diam., glabrous or pubescent, later glabrescent; terminal winter buds ovoid, yellowish sericeous. Stipules sparsely or densely pubescent with short or long yellowish hairs, adnate to the very base of the petiole, stipular scars 3–7(–11) mm long. Leaves thinly chartaceous, dark green, glabrous above, pale green, glabrous to scattered-pubescent with rather long, straight, undulate, crisped and colorless hairs everywhere or along the midrib and nerves beneath, elliptic, (broadly) ovate to obovate, 10–23( 33) × 4.5–10(–14) cm; apex rounded, acute, or short-acuminate, base rounded or broadly cuneate, usually oblique; nerves prominent beneath, in 7–13 pairs. Petiole glabrous or yellowish pubescent, 2–5 cm long. Peduncles glabrous to densely woolly with yellowish hairs, 2.5–3 × 0.7–1 cm, pedicles 1.5–2.5 × 0.3–1 cm. Flowers large, 15–25 cm diam., precocious, slightly fragrant; tepals 12–16, white, or pale rose at the base outside to pink outside, spathulate, oblong-ovate to -obovate, abruptly constricted into a short claw near the base, the outer 3 concave, outspread to reflexed, 6–14 × 4–8 cm, the innermost tepals 3, erect, connivent, enclosing the androecium and gynoecium, 8–10 × 4–6 cm; stamens 2–3 cm long, connective appendage 0.5–1 mm long, anthers laterally dehiscent, filaments purple, minutely pubescent, 4–9 mm long; gynoecium green, 2.5–4 cm long; scar of perianth and stamens on torus ca. 1.5–2 cm long. Fruiting peduncles 2.7–5 × 1–1.2 cm, pedicles 1.5–2.5 × 0.6–1.3 cm. Fruits erect, soon pendent, cylindric, 8.5–17 cm long, ripe carpels packed close to each other; scars of perianth and stamens along the torus 1–2.2 × 1.3–1.5 cm. Seeds 7–9 mm long.

*Distribution.* Northern India, Nepal, Bhutan, China, northern Burma. In CHINA. **Sichuan**: *Tsang H.L. 33747.* **Southern Xizang**: *Kingdon Ward F. 10365.* Western & northern Yunnan (Nujiang–Langchuanjian divide of Weixi Xian, Nujiang divide of Ruili Xian), Salwin–Kui Chiang divide, *Forrest G. 20841*; Mekong–Salwin divide, 28°15′N, *140*; Southeastern Xizang border: Tsarong, *Rock J.F. 23066*; Che-tse-lo, *Tsai H.T. 58573*; Duanqing, above Yangbi, *Sino-British Exped. 166.*

*Ecology.* In mixed forests. Altitude: 2,500–3,500 m. Flowering March–May; fruiting September–October.

*Uses.* Cultivated as an ornamental plant because of its spectacular flowers.

*Collector's notes.* Deciduous shrub or tree; leaves and bud-scales glabrous; flowers pure white, exterior with purple marking at the base, creamy white flushed purplish, creamy yellow, bright rose-pink, pink, precocious, open cup-shaped, fragrant, fleshy, filaments purple, anthers brown.

*Note.* We agree with Dandy that there is no clear separation between *Magnolia campbellii* and *Magnolia mollicomata* (see Dandy, 1928a). The species is misidentified as *Magnolia rostrata* by W. W. Smith (1920).

*Magnolia grandiflora* (non. L., 1759) is the name used by Griffith (1847) for this species.

20. **Magnolia dawsoniana** Rehder & E. H. Wilson in Sarg., Pl. Wilson 1: 397. 1913. TYPE: *E. H. Wilson 1241* (holotype, A; isotypes, BM, K, US).

Deciduous tree to 20 m high and 50 cm diam.; twigs yellowish green, turning reddish brown later, glabrous to sparsely pubescent at 1–3 nodes or internodes below the peduncles, lenticellate. Stipules appressed-pubescent, adnate to very base of the petiole, stipular scars 3–4 mm long. Leaves coriaceous, dark green, glossy, glabrous above, glaucous, usually pubescent with slightly curly, colorless hairs at the junctions between the midrib and nerves and along the veins beneath, obovate, sometimes broadly obovate-elliptic, 7.5–14(–17) × 4.5–8 cm; apex rounded to acute, rarely emarginate, base cuneate to subrounded, usually oblique; midrib impressed above, prominent and becoming brown when dry beneath, nerves conspicuously elevated beneath, in 8–10 pairs, reticulation coarsely netted, prominent, on both sides. Petiole glabrous to minutely pubescent, slender, usually reddish, 1.5–3 cm long. Peduncles glabrous or ± pubescent, 1.5–2 × 0.4–0.7 cm, pedicles 7–12 × 3–4 mm; bracts 2, sparsely yellowish pubescent. Flowers precocious, fragrant, usually horizontal, nodding later; tepals 9–12, white, tinged with pale red outside, subequal, oblong-spathulate to obovate-oblong, 7–11 × 2–5 cm; stamens purple-red, 1–1.8 cm long, anthers laterally or sublaterally dehiscent, connective appendage triangular, ca. 1

mm long, filaments 2.5–3 mm long, gynoecium ca. 1.5 cm; scar of perianth and stamens on torus ca. 8 × 6 mm. Fruiting peduncles ca. 2.2 × 1 cm, pedicles 0.7–1 × 0.7–0.8 cm. Fruits cylindric, slightly contorted as carpels partly abortive, ca. 10.5 × 3 cm; ripe carpels obovate, sparsely lenticellate, apically short-beaked. Seeds oblong, ca. 1 cm long.

*Distribution.* CHINA. **Central and southern Sichuan**: Lu Ding Xian, *Qiao H.R. 1010*; Mt. Tachien lu, *Wilson E.H. 1241*. Northern Yunnan.

*Ecology.* In broad-leaved forest. Altitude: 1,600–2,500 m. Flowering April–May; fruiting September.

*Uses.* Bark used for medicinal purposes.

21. **Magnolia heptapeta** (Buc'hoz) Dandy, J. Bot. 72: 103. 1934. *Lassonia heptapeta* Buc'hoz, Pl. Nouv. Découv. 21, t. 19, f. 1. 1779. TYPE: f. 1 of t. 19 (Buc'hoz, 1779).

*Magnolia denudata* Desr. in Lam. Encycl. 3: 675. 1792. *Magnolia obovata* Thunb., Trans. Linn. Soc. London 2: 336. 1794. *Magnolia obovata* [var.] *α denudata* (Desr.) DC., Syst. Nat. 1: 457, comb. illeg. 1817. TYPE: t. 43, Mokkwuren 1 (Banks, 1791, in BM).

*Magnolia conspicua* Salisb., Parad. Lond. 1: 38, t. 38. 1806. *Yulania conspicua* (Salisb.) Spach, Hist. Nat. Vég. 7: 464. 1839. TYPE: Salisb. t. 38.

*Magnolia yulan* Desf., Hist. Arbr. France 2: 6. 1809. *Michelia yulan* (Desf.) Kostel., Allg. Med.-Pharm. Fl. 5: 1700. 1836. *Gwillimia yulan* (Desf.) C. de Vos, Handb. Boom. Heest. ed. 2: 116. 1887. TYPE: not known.

Deciduous tree to 20 m high and 60 cm diam.; bark dark gray, rough and fissured; young twigs 3–7 mm diam., purple-brown, finely appressed-pubescent, later glabrescent, smooth, sparsely white-lenticellate; terminal winter buds ovoid, densely hairy with long, silky hairs. Stipules sparsely or densely yellowish pubescent, adnate to the base of the petiole, scars 1–4 mm long. Leaves thinly chartaceous, dark green, glabrous to pubescent with straight or slightly undulate hairs along the midrib and nerves or short-scattered-pubescent on the surfaces above, pale green, sparsely to densely pubescent with short or rather long, straight or curly, colorless hairs everywhere or only along the midrib and nerves beneath, obovate to broadly obovate, 8–17.5(–21.5) × 5–10.5(–16) cm; apex rounded to truncate, abruptly short-acuminate, acumen 1–15 mm long, base cuneate or rounded; midrib and nerves visible on both sides, nerves in 7–10 pairs, reticulation coarse, obscured. Petiole appressed-pubescent, glabrescent, 1.3–2.5 cm long. Flowers appearing before the leaves, erect, fragrant, 10–12 cm diam., peduncles 12–20 × 5–7 mm, densely appressed-villous with yellowish hairs, pedicles 4–6 mm long; tepals 9, white, sometimes tinged with purple outside at the base, subsimilar, obovate to spathulate, 6–12 × 2–6 cm; stamens purplish, 10–13 mm long, anthers dehiscing sublaterally, connective appendage narrowly triangular, ca. 1 mm long, filaments 3–4 mm long; gynoecium cylindric, glabrous, 2–2.5 cm long. Fruiting peduncles 12–20 × 6–9 mm. Fruits cylindric, straight or distorted by the abortive carpels, 7.5–15 × 2.5–5 cm; ripe carpels 1–2 cm long, usually white-lenticellate, papilliferous outside, hardly beaked; scars of perianth and stamens along the torus 7–12 × 6–10 mm. Seeds obliquely ovoid to broadly ovoid, ca. 9 × 10 mm.

*Distribution.* CHINA. **Anhui**: Chiu Hwa Shan, *Fan C.S. & Y.Y. Li 261*. **Fujian**: Hinghwa, *Lin Pi 6488*. **Guangdong**: Heungshan, *Chun W.Y. 69*; Yuyuen, *Lamont J. 53089*. **Guangxi**: Quangxian, *Chen Y.L. 192*. **Guizhou**: Gui Yang, *Qian Bei Exped. 89*. **Hunan**: Yang shan, Changning Hsien, *Fan C.S. & Y.Y. Li 191*. **Jiangxi**: Kuling, *Chiao C.Y. 18702*; Lu shan, *Steward A.N. 4730*. **Jiangsu**: Sukow, Haichow, *Hers J 622*. **Zhejiang**: Kwatou, 40 li N of Siachu, *Ching R.C. 1602*; Mo Kan Shan, *Cheo & Wilson 12746*; Tien Mu Shan, *Law Y.W. 1385*; Tsing yuan distr., *Keng Y.L. 453*.

*Uses.* The straight-grained and fine-textured wood is used for furniture and boards; flower buds for medicinal purposes and the extraction of volatile oil; the tree as an ornamental.

*Collector's notes.* Bark brownish gray peeling off in thick plates; flowers white tinged purple at base; fruits green.

*Notes.* Ueda (1986) gave an account of the complicated synonymy. Formerly, this species was known under the name *Magnolia denudata* Desr., but Dandy (1934) changed the name to the older synonym *Magnolia heptapeta*, based on *Lassonia heptapeta* Buc'hoz. Meyer & McClintock (1987) argued that the names *Magnolia heptapeta* and *Magnolia quinquepeta* should be rejected because their types, artistic impressions of the species, are "entirely without botanical credibility." Ueda (1986), but also Treseder (1978), in his standard work on cultivated Magnolias, accepted both names. The nomenclature specialists I consulted agreed that the names *heptapeta* and *quinquepeta* should be used, "otherwise many other names should be rejected too" (H. P. Nooteboom). *Magnolia precia* Correa ex Vent., nomen nudum (Ventenat, 1806), belongs here.

22. **Magnolia sargentiana** Rehder & E. H. Wilson in Sarg., Pl. Wilson. 1: 398. 1913. TYPE: *E. H. Wilson 914* (holotype, A; isotypes, BM, E, GH, K, US).

*Magnolia conspicua* var. *emarginata* Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 38. 1905. *Magnolia denudata* var. *emarginata* Pamp., Bull. Soc. Tosc. Ortic. 20: 200. 1915. *Magnolia emarginata* (Finet & Gagnep.) Cheng, J. Bot. Soc. China 1, 3: 298. 1934. TYPE: *David s.n.* (holotype, P).

*Magnolia sargentiana* var. *robusta* Rehder & E. H. Wilson in Sarg., Pl. Wilson. 1: 399. 1913. TYPE: *E. H. Wilson 923a* (holotype, A; isotypes, K, US).

Deciduous tree to 20 m high and 25 cm diam.; young twigs 4–7 mm diam., yellow-brown, black-brown to gray-brown, glabrous; terminal winter buds ovoid, densely yellowish villous with silky, long hairs, ca. 2.7 cm long. Stipules sparsely to densely appressed-pubescent, adnate to lower base of the petiole, stipular scars 2–5 mm long. Leaves thin-coriaceous, dull green, glabrous, glossy above; pale green, densely appressed-pubescent with rather long, undulate to crisped, colorless hairs, sometimes seemingly glabrous when covered with minutely scattered hairs below; usually inequilateral, obovate, rarely broadly obovate, sometimes elliptic, 10.5–17.5(–22.5) × 5–10(–12) cm; apex acute to rounded, sometimes emarginate or truncate, base usually oblique, cuneate to broadly cuneate; midrib and nerves conspicuously elevated beneath, nerves in 8–12 pairs, reticulation coarsely netted, visible above. Petiole glabrous, 1.5–3.2(–4.7) cm long. Flowers precocious, slightly fragrant, horizontal or nodding, 15–20 cm diam. when fully open; peduncle 20–23 × 6–7 mm, pedicle 12–15 × 5–6 mm (but absent in *H.T. Tsai 51831*), glabrous to densely yellowish villous; tepals 10–12, subsimilar, purplish red outside and white to pale rose inside, spathulate to obovate, with narrow base, 6.5–9.5 × 2–3 cm; stamens purplish, 14–17 mm long, anthers dehiscing sublaterally, connective appendage triangular, ca. 1 mm long, filaments 3–4 mm long; gynoecium green, cylindric, 8–12 × 3 mm; carpels many. Fruiting peduncles glabrous to hairy, ca. 2–3.5 × 1 cm, pedicles 1.2–2.2 × 0.6–1 cm. Fruits cylindric, 3–20.5 × 1.5—2.5 cm, erect to curved; ripe carpels subglobose, 7–22 mm long, apex short-beaked; torus with scars of perianth and stamens 1.2–1.5 × 1–1.2 cm. Seeds subcordate, 8–12 × 7–10 mm.

*Distribution.* CHINA. **Sichuan**: Wa shan, *Wilson E.H. 914*; Tian Quan, *Tsang H.L. 34828*; near Xizang border, *Pratt A.E. 798*; Mt. Omei, *Chow H.C. 9777*; O-pien hsien, *Liu Y.S. 2191*; Paohsing hsien, *Chu K.L. 3908*. **Yunnan**: between Tsian and Ta Kuan, *Tsai H.T. 50843*; Wen-shan Hsien, *51831*.

*Ecology.* In broad-leaved forest. Altitude: 1,600–2,500 m. Flowering April–May; fruiting September.

*Uses.* Bark for medicinal purposes.

*Note.* *Magnolia sargentiana* var. *robusta* differs from *Magnolia sargentiana* var. *sargentiana* in its larger leaves and bigger flowers and fruits. Except for this difference in size, we could not find any characters to distinguish them. The variety, therefore, is here abolished.

23. **Magnolia sprengeri** Pampanini, Nuovo Giorn. Bot. Ital. 22: 295. 1915. TYPE: *Silvestri 4104* (holotype, FI not seen).

*Magnolia denudata* Desr. var. *purpurascens* Rehder & E. H. Wilson in Sarg., Pl. Wilson 1: 401. 1913. *Magnolia conspicua* var. *purpurascens* sensu Bean, Kew Bull. 1920: 119. 1920. TYPE: *Wilson 373* (lectotype, selected here, A; isolectotypes, E, K, US).

*Magnolia diva* Stapf ex Dandy in Millais, Magnolias 120. 1927. *Magnolia sprengeri* var. *diva* Stapf, Bot. Mag. (Curtis) 153: t. 9116. 1927. TYPE: *E. H. Wilson 21* (lectotype, selected here, K; isolectotypes, A, K, NY).

*Magnolia denudata* Desr. var. *elongata* Rehder & E. H. Wilson in Sarg., Pl. Wilson 1: 402 sub t. 9116. 1913. *Magnolia sprengeri* var. *elongata* (Rehder & E. H. Wilson) Johnstone, Asiatic Magnolias in Cultivation: 87. 1955. TYPE: *E. H. Wilson 345* (holotype, A; isotypes, E, GH, K, US).

Deciduous tree to 20 m high and 18 cm diam.; bark black-gray, falling in small flakes when old; young twigs 3–5 mm diam., yellow to yellow-brown, becoming purple-brown later, glabrous and sparsely lenticellate, old twigs gray-black, fissured; terminal winter buds broadly ovoid, 2.8–3 × 1.8–2.4 cm, densely yellowish villous with straight and silky hairs. Stipules densely pubescent with appressed yellowish white hairs, glabrescent, adnate to the base of the petiole, scars 1–2(–13) mm long. Leaves coriaceous, dark green, glabrous to sparsely pubescent along the midrib and nerves above; pale green, glabrous to appressed-pubescent with fine, short, straight and colorless hairs over the entire surface or covered with long hairs along the midrib only, glabrescent beneath; obovate to narrowly obovate, 7–14.5(–22) × 2.5–7.5(–15) cm; apex rounded, sometimes truncate and short-acuminate with 5–15-mm-long acumen, base cuneate to narrowly cuneate; midrib and nerves conspicuously elevated below, the latter in 6–8 pairs, reticulation coarse, visible on both sides. Petiole slender, glabrous or villous near the base of the blades, 1–3.5 cm long. Peduncles yellowish sericeous with straight hairs, glabrescent, stout, 10–17 × 6–8 mm, pedicles 4–8 × 4–5 mm. Flowers appearing together

with the leaves, saucer-shaped, fragrant, erect, to 20 cm diam. when fully open; tepals 12(–14), subsimilar, spathulate to oblong-obovate, 5–12(–14) × 1.5–4(–6.5) cm, pure white or sometimes with red at the base, rose outside and white inside with flush of red to purple-striate; stamens red, numerous, 1.5–1.7 cm long, anthers sublaterally dehiscing, connective appendage triangular, 1–2 mm long, filaments 5–7 mm long; gynoecium cylindric 2–2.5 × 0.3–0.4 cm, carpels ellipsoid. Fruiting peduncles 10–20 × 7–9 mm, pedicles 4–9 × 5–6 mm. Fruits cylindric and often distorted by the abortive carpels, 6–10 cm long, ripe carpels without beak, 7–15 mm long. Seeds subovoid to subcordiform, 8–12 × 7–9 mm, torus with the scars of perianth and stamens 8–10 × 8–10 mm.

*Distribution.* CHINA. **Guizhou**: Lei Gong Shan, *Li Y.K. 8921*. **Henan**: Lushih, Lao kiun shan, *Hers J 1159*. **Hubei**: Changyang Hsien, *Wilson E.H. 444*; Hsing shan hsien, *373*; Ichang, *Henry A 2522*; Patung hsien, *Chow H.C. 334*. **Hubei-Sichuan (Metasequoia area)**: *Cheng W.C. & C.T. Hwa 1049*; Shennongjia forest distr., Duanjiangping, *Sino-Amer. Bot. Exped. 1181*. **Sichuan**: Tchen Kéou Tin, *Farges R.P. 94*; Chin Fu Shan, *Pei C., 10242*; Mt. Omei, *Liu Y.S. 1174*. **Yunnan**: Likiang, *Ching R.C. 21681*. Also recorded from Shaanxi and southern Gansu.

*Ecology.* In evergreen broad-leaved or mixed forests. Altitude: 1,200–2,000 m. Flowering March; fruiting June–July.

*Uses.* Flowers and bark used for medicinal purposes; the tree is cultivated as an ornamental.

24. **Magnolia zenii** Cheng, Contr. Biol. Lab. Sci. Soc. China, Bot. Series 8: 291, f. 20. 1933. TYPE: *W. C. Cheng 4233* (holotype, PE).

*Magnolia elliptilimba* Law & Gao, Bull. Bot. Res. (China) 4(4): 190, t. 1. 1984. TYPE: China. Henan: Nanzhao Xian, 12 Mar., 1983, alt. 400–800 m, *Z. Y. Gao 0129* (in Herb. Henan Inst. Biol. not seen).

Deciduous tree to 7 m high; bark gray, smooth; young twigs purple-brown, glabrous, sparsely lenticellate. Terminal winter buds narrowly ovoid, densely sericeous with long hairs. Stipules hairy, adnate to the base of the petiole, scars 3–7 mm long. Leaves chartaceous, dull green, glabrous above; pale green, covered with curly, long hairs along midrib and nerves beneath; obovate, 7–16 × 3–7 cm; apex abruptly short-acuminate, base broadly cuneate to blunt; nerves in 8–12 pairs. Petiole villous, glabrescent, 6–15 mm long. Flowers precocious, cup-shaped, fragrant, 10–12 cm diam., peduncles densely long-hairy, 2–8 mm long; tepals 9–12, subequal, spathulate, 7–8 × 3–4 cm, at first purple-red, becoming white above the middle and purplish toward the base when fully open, the inner tepals 6, narrow; stamens purple, 1.5–1.7 cm long, anthers dehiscing laterally, connective appendage triangular, ca. 1 mm long; filaments ca. 4 mm long; gynoecium cylindric, ca. 2 cm long, carpels ca. 4 mm. Fruits cylindric, 5–20 × 1–2.5 cm; ripe carpels subglobose, papilliferous, apex obtuse.

*Distribution.* CHINA. **Henan**: Nan Zhao Xian, *Gao Z.Y. 126*; Kiangsu, Paochuashan, *Cheng W.C. 4233*.

*Ecology.* In forest. Altitude: 250–300 m. Flowering April–May; fruiting August–September.

*Uses.* Tree cultivated as an ornamental.

*Note.* Only the type specimen of *Magnolia zenii* was available. We have not seen the type of *Magnolia elliptilimba*, but we reduce it to synonymy of *M. zenii* based on the description and the geographic distribution.

**Ib-2. Magnolia** section **Buergeria** (Siebold & Zuccarini) Dandy in Camellias and Magnolias Conf. Report: 73. 1950. *Buergeria* Siebold & Zucc., Abh. Math.-Phys. Cl. Kön. Bayer. Ak. Wiss. 4, 2: 186. 1846. TYPE SPECIES: *Magnolia stellata* (Siebold & Zucc.) Maxim. (*Buergeria stellata* Siebold & Zucc.).

Flowers appearing before the leaves (or with the leaves), pink (inner tepals sometimes tinged with rose or purple). Tepals very unequal, those of the outer whorl calycoid.

KEY TO THE SPECIES OF *MAGNOLIA* SECTION *BUERGERIA*

1. Inner tepals 4–5 cm long; connective appendage of anthers 2–3 mm long; filaments 2.5–3.5 mm; peduncles 7–11 × 4–5 mm. ..... 25. *Magnolia biondii*
1. Inner tepals 3.2–10 cm; connective appendage of anthers 0.5–1 mm long; filaments 2–5 mm long; peduncles 2–12 × 2–5 mm. ..... 2
2(1). Peduncles 2–10 × 2–3 mm; inner tepals 3.2–9 cm. ..... 3
2. Peduncles 10–12 × 4–5 mm; inner tepals 6.5–10 cm; connective appendage of anthers 1 mm; filament 3 mm. 26. *Magnolia cylindrica*
3(2). Inner tepals 5–9 cm; connective appendage of anther 0.5 mm; filament 2 mm. ..... 27. *Magnolia kobus*
3. Inner tepals 3.2–6.5 cm; connective appendage of anther 1 mm; filament 2–5 mm. ..... 28. *Magnolia stellata*

25. **Magnolia biondii** Pampanini in Nuovo. Giorn. Bot. Ital. 17: 275. 1910. SYNTYPES: Scia-men-kvu, ca. 900 m alt., *Pavol. 734*, *734a* (not seen).

*Magnolia conspicua* Salisb. var. *fargesii* Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 38. 1905. *Magnolia denudata* Desr. var. *fargesii* (Finet & Gagnep.) Pamp., Bull. Soc. Tosc. Ortic. 20: 200 1915. *Magnolia fargesii* (Finet & Gagnep.) Cheng, J. Bot. Soc. China 1, 3: 296. 1934. TYPE: *Farges 1300* (holotype, P; isotype, K).

*Magnolia aulacosperma* Rehder & E. H. Wilson in Sarg., Pl. Wilson. 1: 396, 408. 1913. TYPE: *E. Wilson 361* (holotype, A; isotypes, K, US).

*Magnolia biondii* f. *purpurascens* Law & Gao, Bull. Bot. Res. (China) 4(4): 192, t. 2. 1984. TYPE: *Gao, Z. Y. 0122* (in Herb. Henan Inst. Biol.).

Deciduous tree to 12 m high and 60 cm diam.; bark pale gray, smooth; twigs slender, glabrous to appressed-pubescent, glabrescent; terminal winter buds ovate, densely yellowish villous. Stipules yellowish to white pubescent with short hairs, adnate to the lower base of the petiole, stipular scars 1–4 mm long. Leaves chartaceous, dull green above, pale green, usually pubescent with long, straight, undulate, crisped and colorless hairs along the midrib and nerves to glabrous beneath, ovate, narrowly obovate-elliptic to oblong-elliptic, rarely oblanceolate, 10–21.7 × 3.5–11 cm; apex acute to acuminate, base cuneate to rounded; nerves in 10–15 pairs. Petiole 1–2 cm long. Peduncles 7–11 × 4–5 mm, densely pubescent with long, yellowish hairs, pedicles very short, ca. 2 mm long. Flowers precocious, 6–8 cm diam., fragrant; tepals 9, the outer 3 nearly linear, 8–11 mm long, the inner tepals 6, white, spathulate, 4–5 × 1.3–2.5 cm, the innermost ones smaller than the others, abaxial faces tinged with purple at the base; stamens 8–10 mm long, connective appendage 2–3 mm long, filaments thick, purple outside, white inside, 2.5–3.5 mm long. Fruits cylindric, ± contorted, 6–14.5 cm long; fruiting peduncles ± pubescent, glabrescent, 1–1.2 × 0.6 cm, pedicles 4–6 mm long; ripe carpels black, globose, compressed laterally, densely papilliferous, scars of perianth and stamens along the torus 9–10 × 6–7 mm.

*Distribution.* CHINA. **Henan**: Yudong Xian, *Pucha Biaoben 23252*; Lushin, Tungho, *Hers J 991*; Sunghsien, Sankuanmiao, *541*; Yungning, Tsi Li Ping, *1343*. **Hubei**: Li-chuan, Tuan-Pao-Shih, *Hwa C.T. 104*; Liang Dung Gonn, *Chun W.Y. 4409*. **Shaanxi**: Nanwutai forest S of Hsingan (Si-an), *Fenzel G. 2893, 2951*. **Sichuan**: Wan-Hsien, Mou-Tao-Chi, Kan-Tsao-Ping, *Hwa C.T. 65*; Tchen Keou Tin, *Farges R.P. 1300*. Also reported from Gansu (W. Qinling) and Shaanxi (Dabashan).

*Ecology.* In forest. Altitude: 400–2,000 m. Flowering March; fruiting September.

*Uses.* Wood used for furniture and general construction work; flower buds for medicine, flowers for volatile oil; tree grown as an ornamental.

*Collector's notes.* Bud silky; flowers white; fruits purplish red tinged.

*Note.* Several new species and varieties of *Magnolia* were recently published in Henan. Their descriptions basically fit in *Magnolia biondii*. Unfortunately, we have not seen their type specimens or other collections; therefore, we have dealt with them under "Dubious Species." Pavolini (1908) misidentified this species as *Magnolia obovata* Thunb.

26. **Magnolia cylindrica** E. H. Wilson, J. Arnold Arbor. 8: 109. 1927. TYPE: *R. C. Ching 2949* (holotype, A; isotypes, E, K, US).

Deciduous tree to 10 m high; bark white-gray, smooth; young twigs purple-brown to dark purple, yellowish appressed-pubescent, sometimes glabrous; terminal winter buds ovate, yellowish sericeous with long hairs. Stipules densely pubescent, adnate to the petiole, stipular scars 2–7(–9) mm long. Leaves chartaceous to subcoriaceous, dark bright green, glabrous above, greenish, appressed-pubescent with fine, short, straight, and colorless hairs beneath, elliptic, narrowly obovate-elliptic, narrowly obovate to obovate, 8–15 × 3–9 cm; apex acute to short-acuminate, base cuneate or narrowly cuneate; nerves fine, prominent below, in 8–11 pairs. Petiole with same indument as young twigs, 7–10(–24) mm long. Peduncles densely yellowish villous, 1–1.2 × 0.4–0.5 cm, pedicles 5–6 × 2–3 mm long; bracts 2, gray-pubescent outside. Flowers precocious; tepals 9, the outer 3 subulate, 2–2.5 × 0.5–1 cm, the inner tepals 6, white, tinged pale rose outside at the base, broadly spathulate to obovate, 6.5–10 × 2.5–4.5 cm, the innermost 3 tepals erect; stamens ca. 7 mm long, anthers laterally dehiscent, connective appendage triangular, ca. 1 mm long, filaments purple, glabrous, ca. 3 mm long; gynoecium green, cylindric, ca. 1.2 cm long. Fruiting peduncles pubescent, 1 1.5 × 0.5–0.6 cm, pedicles 5–10 × 4 mm. Fruits cylindric, 5–7.5 × 1.8–2.5 cm, pendulous.

*Distribution.* CHINA. **Anhui**: Bai Ma Zhai, Lan Ni Ao, Jonzhai, *Yao K. 9006*; Wang Shan, *Ching R.C. 2949*. **Fujian**: near Zhejiang border, *Ching R.C. 2501*. Also reported from northern Jiangxi and western Zhejiang.

*Ecology.* In forest. Altitude: 300–800 m. Flowering May–June; fruiting August–September.

27. **Magnolia kobus** DC., nom. cons. prop., Syst. Nat. 1: 456. 1817. *Magnolia glauca* var. α Thunb., Fl. Jap.: 236, 378, 1784b. *Magnolia tomentosa* Thunb., Trans. Linn. Soc. London.

2: 236. 1794a. *Yulania kobus* (DC.) Spach, Hist. Veg. 7: 467. 1839. TYPE: *Kaempfer* (lectotype, selected by Rehder (1930), BM).

*Magnolia praecocissima* Koidz., Bot. Mag. (Tokyo) 43: 386. 1929. *Buergeria obovata* Siebold. & Zucc. (non *Magnolia obovata* Thunb. 1794), Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4, 2: 187. 1845. TYPE: *Von Siebold, left half of L-908-126-1027* (lectotype, selected by Koidzumi (1929), L.).

This specimen has disappeared in the Leiden Herbarium. Ueda (1985) provided a photo of it, and as long as the specimen has not been found, that is the only trace of a type.

Deciduous tree to 20 m high, often branching near the base; bark gray, rough, fissured; young twigs 1.5–3 mm diam., green, soon turning purple-brown, glabrous or somewhat puberulent; terminal buds ovate, yellow-sericeous with long hairs. Stipules adnate to the base of the petiole, stipular scars 3–7(–10) mm long. Leaves dark green, white pubescent at the base of midrib above, gray-green, white pubescent along the nerves and at junctions with the nerves beneath, obovate-elliptic, ca. 8–17 × 3.5–9.5(–11) cm; apex abruptly acuminate, base narrowly cuneate, slightly decurrent; midrib and nerves impressed when dry above; nerves in 8–12 pairs, margin slightly undulate. Petiole white villous, ca. 1–2.6 cm. Flowers appearing before the leaves, white, fragrant; peduncles 7–10 × 2–2.5 mm, glabrous to hairy on nodes, pedicles 1.4–4 mm long; bracts 2–3, pubescent outside; flower buds narrowly ovate, flowers ca. 9–10 cm diam. when fully open, tepals 9, outer tepals 3, greenish or white, triangular-linear, 5–15 × 2–3 mm, inner tepals white, sometimes flushed with red at the base, spathulate, ca. 5–7(–9) × 1.5–3 cm; stamens ca. 8–10 mm long, anthers dehiscing latrorsely or sublatrorsely, filaments red, ca. 2 mm; connective appendage triangular, ca. 0.5 mm long; gynoecium green, cylindric, ca. 1–1.5 cm long. Fruiting peduncles 8–10 × 3–6 mm, pedicles 6–9 × 3–4 mm. Fruits cylindric, 3.5–11 cm, often contorted by sterile carpels; carpels nearly oblong, white lenticellate. Scars of perianth and stamens 5–6 × 3–5 mm. Seeds subglobose, 10–9 × 9–8 mm.

*Distribution.* Native of Japan and southern Korea, cultivated in Qingdao, Nanjing, and Hangzhou.

*Uses.* Wood used for general construction work and furniture, tree grown as an ornamental.

*Note.* The Kaempfer collection of *Magnolia* named "kobus," from which Kaempfer t. 42 (1791) is drawn, forms the main part of the protologue of Thunberg's (1784b) *Magnolia glauca* var. α. *Magnolia tomentosa* Thunb. (1794a) is based on *Magnolia glauca* Thunb. var. α, with citation of Kaempfer t. 42. So far there is no doubt about the identity of *Magnolia tomentosa*, especially because Thunberg visited London and studied Kaempfer's collections and drawings. But Thunberg (1794b) published a list of specimens kept in UPS, which includes *Magnolia tomentosa*; this name is, in his handwriting, written on sheet number 12887. This specimen, however, appears to be *Magnolia stellata*. If Ueda's (1986) interpretation, that Thunberg himself selected number 12887 as the type of *Magnolia tomentosa*, is correct, *Magnolia tomentosa* becomes the legitimate name for *Magnolia stellata*. The latter name is then superfluous. Thunberg (1805) also published a drawing of sheet number 12887, with the name *Magnolia tomentosa* but without a description. This has commonly been cited as *Magnolia tomentosa* Thunb. (1805), non Thunb. (1794a).

De Candolle (1817), when describing *Magnolia kobus*, cited Banks ic. Kaempfer t. 42 first in the protologue, and then *Magnolia glauca* Thunb. var. α. He cited *Magnolia tomentosa* Thunb. with a question mark. De Candolle also cited *Magnolia gracilis* Salisb. Salisbury (1806) described *Magnolia gracilis* with an excellent figure based on a collection that was sent to De Candolle and is kept in G-DC. This collection appears to be *Magnolia quinquepeta*. However, because Salisbury cited *Magnolia tomentosa* without excluding its type, *Magnolia gracilis* is a superfluous name of *Magnolia tomentosa*. De Candolle, possibly not knowing what *Magnolia tomentosa* was, gave a new name to *Magnolia gracilis* Salisb.: *Magnolia kobus* DC. Because De Candolle cited *Magnolia tomentosa* with a question mark, it could be assumed that he excluded the type of that species, and that *Magnolia kobus* DC. is a superfluous name of *Magnolia quinquepeta* (Buc'hoz) Dandy (1934), based on *Lassonia quinquepeta* Buc'hoz (1779). This was Ueda's (1985, 1986) opinion, and Koidzumi's (1929). Koidzumi assumed that the type of *Magnolia gracilis* Salisb. was also the type of *Magnolia kobus* DC. He therefore adopted a nomen novum, *Magnolia praecossima*, for the species up to then known as *Magnolia kobus*. His name was based on a synonym, *Buergeria obovata* Siebold. & Zucc. (non *Magnolia obovata* Thunb., 1794a). However, it is also possible to exclude *Magnolia gracilis* Salisb. from *Magnolia kobus* DC. Then the latter is typified with the type of *Magnolia tomentosa* Thunb.

In that case there are two possibilities. If *Magnolia tomentosa* Thunb. is lectotypified with *Thunberg 12887*, *Magnolia kobus* DC. is a superfluous name for *Magnolia tomentosa* Thunb. and is the species hitherto known as *Magnolia stellata* (Siebold & Zucc.) Maxim. (1872), based on *Buergeria stellata* Siebold & Zucc. (1845). As pointed out above, *Magnolia stellata* is then a superfluous name for *Magnolia tomentosa* Thunb. If *Magnolia tomentosa* Thunb. is lectotypified with the collection of Kaempfer, as done by Rehder (1930), *Magnolia kobus* DC. is a superfluous name for *Magnolia tomentosa* Thunb. This is rejected by Ueda (1986), who stated that Rehder's lectotypification was contrary to the rules because he would have selected it mechanically. Because Rehder gave ample justification for his choice, we reject that he chose mechanically. We accept *Magnolia kobus* DC. as the name for this species, and we propose both *Magnolia kobus* and *Magnolia stellata* be conserved.

28. **Magnolia stellata** (Siebold & Zucc.) Maxim., nom. cons. propos., Bull. Acad. Sci. St.-Petersburg 17: 419. 1872. *Magnolia kobus* DC. f. *stellata* (Siebold & Zucc.) Blackb., Popul. Gard. 5, 3: 68. 1954. *Magnolia kobus* var. *stellata* Blackb., Amatores. Herb. 17: 2. 1955. *Buergeria stellata* Siebold & Zucc., Abh. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. 4, 2: 186, t. IIa. 1845. *Talauma stellata* (Siebold & Zucc.) Miq., Ann. Mus. Bot. Lugduno-Batavum 2: 257. 1866. TYPE: *Von Siebold L-908-126-701, -750* (L not seen).

The type was photographed at L for Ueda's (1985) publication. The specimen had not yet been incorporated in the family at the time the Rijksherbarium moved to another building. The type has never been seen again.

*Magnolia halleana* Parsons ex Robinson, Gard 13: 572, f. opp. 572. 1878. TYPE: probably the figure.

*Magnolia stellata* var. *keiskei* Makino, Bot. Mag. (Tokyo) 26: 82. 1912. *Magnolia keiskei* (Makino) Ihrig, Arb. Bull. Univ. Wash. 11, 2: 33. 1948. TYPE = plate cited by Makino.

*Magnolia stellata* var. *rosea* Arnott ex Veitch ex Hu, Man. Econ. Pl. 1: 383. 1955. *Magnolia rosea* (Veitch) Ihrig, Arb. Bull. Univ. Wash. 11,2: 34. 1948. *Magnolia kobus* DC. f. *rosea* (Veitch) Blackburn, Popul. Gard. 5, 3: 73. 1954.

Deciduous large shrub or treelet to 5 m high; young twigs slender, 2–3 mm diam., brown-purple to black-purple, sometimes gray-black, densely appressed-pubescent with long, gray or yellowish hairs, glabrescent, smooth, old twigs brown, glabrous, glabrescent. Stipules densely gray pubescent with silky hairs, adnate to the petiole, stipular scars as long as the petiole, 3–14 mm. Leaves thinly chartaceous, dark bright green, glabrous above; pale green, glabrous below, narrowly obovate to obovate, occasionally ovate, 7–11 × 2–5.6 cm; apex obtuse to acute, base cuneate to attenuate, usually decurrent along the petiole, rarely rounded; margin sparsely pubescent; midrib and nerves finely pubescent above, densely villous, glabrescent beneath; nerves fine, visible below, in 10–14 pairs, reticulation coarse, hardly visible on both sides. Petiole covered with same indumentum as the stipules, glabrescent later, 3–14 mm long. Flowers appearing before and after the leaves, white or rose, fragrant, to 10 cm diam.; peduncles densely gray villous, 2–6 × 2–3 mm, pedicle 0.2–4 × 3 mm; tepals 12–18, very unequal, usually narrowly obovate to spathulate, apically obtuse, rarely acute, basally broad, 3.2–6.5 × 0.7–1.7 cm; stamens 6–11 mm long, anthers dehiscing latrorse or sublatrorse, connective appendage triangular, ca. 1 mm long, filaments 2–5 mm long; gynoecium cylindric, 7–10 × 2–3 mm; carpels many. Fruiting peduncles densely hairy, 3–6 × 3–4 mm. Fruits cylindric or irregularly shaped abortive carpels, 2–4.5 × 1–1.5 cm; ripe carpels subglobose, 7–12 mm long, with short beaks at the apex; scars of perianth and stamens along the torus 2–6 × 3–5 mm.

*Distribution.* Native to Japan, cultivated in Nanjing.

*Uses.* Tree grown as an ornamental.

*Note.* Ueda (1985, 1986) gave an account as to why the common star Magnolia, *Magnolia stellata*, should be legitimately named *Magnolia tomentosa*. However, because of the economic importance of the species it will be proposed as nomen conservandum. See also the notes under *M. kobus*.

**Ib-3. Magnolia** section **Tulipastrum** (Spach) Dandy, in Camellias and Magnolias, Conf. Report: 74. 1950. *Tulipastrum* Spach, Hist. Natur. Veget., Phanerog. 7: 481. 1839. TYPE SPECIES: *Magnolia acuminata* L.

Flowers appearing together or after the leaves, pink, purple, or red. Tepals very unequal (those of the outer whorl calycoid).

29. **Magnolia quinquepeta** (Buc'hoz) Dandy, J. Bot. 72: 103. 1934. *Lassonia quinquepeta* Buc'hoz, Pl. Nouv. Découv. 2: f. 2 of t. 19. 1779. TYPE: f. 2 of t. 19 (Buc'hoz, 1779).

*Magnolia glauca* [var.] β Thunb., Fl. Jap.: 236, 378, 1784. *Magnolia liliiflora* Desr. in Lam., Encycl. 3: 675, "*liliflora.*" 1792. Ohwi, Fl. Jap. rev. ed.: 649, incl. var. *gracilis.* 1978. *Magnolia obovata* Thunb., Trans. Linn. Soc. London 2: 336, nom. superfl. illeg. 1794a. *Yulania japonica* Spach, Hist. Nat. Vég. 7: 466, nom. et comb. illeg. 1839. TYPE: t. 44, Mokkwurén 2 (Kaempfer, 1791, BM).

*Magnolia purpurea* Curtis, Bot. Mag. (Curtis) 11: t. 390. 1797. TYPE: t. 390.

*Magnolia discolor* Vent., Jard. Malmaison: t. 24. 1803. TYPE: t. 24.

*Magnolia gracilis* Salisb., Parad. Lond. 2: 87, t. 87, nom. illeg. 1807. *Magnolia liliflora* var. *gracilis* (Salisb.) Rehder in L. H. Bailey, Stand. Cycl. Hort. 4: 1968. 1916. TYPE: *Salisbury s.n.* (G-DC).

*Buergeria obovata* Siebold & Zucc., Abh. Math.-Phys. Cl. Königl. Bayer, Akad. Wiss. 4,2: 187. 1845. *Talauma ?sieboldii* Miq. in Ann. Mus. Bot. Lugduno-Batavum 2, 9: 257, 1866. *Talauma obovata* (Siebold & Zucc.) Benth. & Hook. f. ex Hance, J. Bot. 20: 2. 1882 (non Korthals, 1851). TYPE: *Von Siebold right half of L-908-126-1027* (L).

Deciduous shrub to 3.5 m high; bark gray-brown; young twigs 2–4 mm diam., dark purple, glabrous or sometimes hairy on a few nodes near the peduncles, smooth, sparsely lenticellate, old twigs gray-purple and longitudinally fissured; terminal winter buds ovoid, 12–14 × 5–6 mm, yellowish sericeous. Stipules densely yellowish to yellowish white pubescent, adnate to the entire petiole, scars 3–15 mm long. Leaves membraneous to chartaceous, dark green, glabrous, sparsely pubescent over the surfaces or only along the midrib above, pale green, glabrous to pubescent with long, undulate to rarely crisped, colorless hairs along the midrib and the nerves below, broadly elliptic to obovate, 6–15(–26) × 3–7(–10) cm; apex acute to acuminate with short or long acumen, base cuneate to attenuate, usually decurrent along the petiole; midrib and nerves prominent beneath, nerves in 8–10 pairs. Petiole pubescent, glabrescent, ca. 3–15 mm long. Flowers appearing with and after the leaves, slightly fragrant; peduncles glabrous or densely villous with silky, yellowish hairs, glabrescent, 5–20 × 6–8 mm, pedicles 10–12 × 5–7 mm, sometimes absent; bracts densely yellowish sericeous, 11 cm long; tepals 9, the outer 3 subulate, occasionally ovate, greenish to purplish, 10–27 × 4–8 mm, the inner tepals 6, spathulate to obovate, purplish outside and white inside, 5.5–9 × 2.5–4.5 cm; stamens purple-red, 8–10 mm long, anthers dehiscing laterally, connective appendage triangular, filaments purple, ca. 2 mm long; gynoecium cylindric, purplish, 1.2–1.4 × 0.4 cm, carpels many. Fruiting peduncles 10–20 × 3–6 mm, pedicles 3–8 × 3–4 mm long. Fruits cylindric, erect to curved as the carpels partly abortive, 3–6.5 × 1–2 cm; ripe carpels ellipsoid to subglobose, 8–15 mm long, gray-lenticellate outside, short-beaked; torus with the scars of perianth and stamens 8–12 × 5–7 mm. Seeds subcordate, ca. 10 × 7 mm.

*Distribution.* CHINA. **Hubei**: Sichuan, Jiang Jin, *Chen S.J. et al. 840055*; Chengtu, *Fang W.P. 13256*; Kun Hsien, *Wang F.T. 20793, Chiao C.Y. & C.S. Fan 444.* **Yunnan**: N end Lichiang valley, 27°5′N, *Forrest G. 2174*; Shweli–Salwin divide, 25°48′N, 98°48′E, *24700*; Tien chin pu valley, 25°30′N, *5539.* Widely cultivated.

*Ecology.* Flowering March–April; Fruiting August–September.

*Uses.* Flower buds and bark used for medicinal purposes, the tree as an ornamental.

*Note.* Ueda (1985) explained the complicated synonymy. The species was formerly known as *Magnolia lili(i)flora.* The name *Magnolia obovata* Thunb. has also been used for this species for a long time.

See also the note under *Magnolia heptapeta.*

*Magnolia hirsuta* Thunb. (1794b, 1824), based on *Thunberg 12884*, is a nomen nudum.

**Ic. Magnolia** subgenus **Talauma** (Juss.) Pierre, Fl. For. Cochinch. 1: sub t. 1. 1880. TYPE SPECIES: *Magnolia plumierii* Schwartz.

Evergreen tree. Stipular scars up to the apex of the petiole. Anthers introrse. Fruits with connate carpels, the apical parts of the carpels falling off leaving the seeds exposed, hanging from the thread-like funiculus.

**Ic-1. Magnolia** section **Blumiana** Blume, Fl. Java Magnol.: 32. 1829.

Leaves evenly distributed; midrib prominent above, at least toward base. Flowers bisexual; tepals subequal; connective produced into a short or long appendage, triangular. Gynoecium not stipitate. Fruits with connate carpels. When mature the apical parts of the carpels circumscissile and falling, dehiscing along the dorsal suture or not, the basal parts remaining adnate to the torus, or apical parts falling in irregular masses.

30. **Magnolia candollii** (Blume) H. Keng var. **obovata** (Korth.) Nooteboom, Blumea 32: 374. 1987. *Talauma obovata* Korth., Ned. Kruidk. Arch. 2, Versl.: 98. 1851. TYPE: Sumatra Gunung Pamatton, *Korthals s.n.* (lectotype, selected here, L sheet no. 925.250-739; isolectotype, BO).

*Talauma hodgsoni* Hook. f. & Thomson, Fl. Ind. 74. 1855. TYPE: Sikkim, 2,000–5,000 ft., *J. D. Hook s.n.* (holotype, K; isotype, L).
*Talauma oblanceolata* Ridley, Fl. Malay Penins. 5: 286. 1925. TYPE: *H. N. Ridlley 15590* (K. SING).
*Talauma betongensis* Craib, Kew Bull. 1925: 7. 1925. *Magnolia betongensis* (Craib) H. Keng, Gard. Bull. Sing. 31: 129. 1978. TYPE: *Kerr 7449* (holotype, K; isotype, BM).
*Talauma sclerophylla* Dandy, J. Bot. 66: 47. 1928. TYPE: *Haviland 3148* (holotype, BM; isotype, K).
*Talauma levissima* Dandy, Kew Bull. 1928: 191. 1928. TYPE: *H. N. Ridley 9047* (holotype, K; isotype, SING).

Tree to 25 m high; young twigs whitish, stout, ca. 1 cm diam., glabrous. Stipules adnate to the petioles, stipular scars from up to about halfway the length of the petioles to nearly as long as the petioles. Leaves coriaceous, glabrous, obovate or sometimes elliptic, 17–50 × 8–22 cm; apex rounded to slightly acuminate, base cuneate, usually attenuate; nerves in 9–25 pairs, curved upward and meeting in an intramarginal vein, reticulation rather coarse, sometimes obscure. Petiole 2.5–7 cm long. Peduncles glabrous, 3–12 × 0.5–1.3 cm, with 2–18 nodes, pedicles absent or very short. Tepals 9, thick fleshy, the outer 3 greenish outside, sometimes reflexed in mature flowers, 1.5–5(–6.5) × 1–2 cm, the inner tepals 6, creamy white, erect, shorter than to as long as the outer tepals; stamens 1.2–3 cm long, connective appendage triangular to subulate, 1–3 mm long, filaments 1–3 mm long; gynoecium ellipsoid, 1–2 cm long, carpels 10–100, pubescent, the styles long, becoming woody spines to 15 mm in fruits but sometimes caducous; scars of perianth and stamens on torus ca. 5 × 8 mm. Fruits ellipsoid, 5–15 × 4–7.5 cm.

*Distribution.* Tibet, Sikkim, Nepal, Assam (Khasia), Burma, Thailand, and Malesia. In CHINA. **Southern Yunnan:** *D.T. Tao 413.*

*Ecology.* In evergreen broad-leaved forest. Altitude: 800–1,500 m. Flowering May–June; fruiting August–September.

*Notes.* Without fruits this species is hard to distinguish from *Magnolia henryi* Dunn. The latter species has, as typical in subgenus *Magnolia*, follicles that dehisce dorsally. In subgenus *Talauma* the apical parts of the carpels fall off entirely, leaving the axis with the carpellar scars and red seeds hanging from a funiculus. *Magnolia henryi* is therefore intermediate between the two subgenera. *Talauma luchuensis* Law (manuscript), from Yunnan (*D.T. Tao 413*, KUN), is *Magnolia candollii* var. *obovata*, with the developing fruits abnormally precocious.

*Magnolia candollii* var. *obovata* was erroneously identified as *Manglietia glauca* (non Blume, 1823) by Ridley (1922) for the collection of L. M. Bell & Haniff and by Ridley (1913) and Merrill (1921a) as *Talauma candollei* (non Blume, 1823).

## Hybrids and Cultivated Species of Sections Not Native to China

31. **Magnolia ×soulangiana** Hamel, Ann. Soc. Hort. Paris 1: 90. 1827. *Magnolia yulan* var. *soulangiana* (Hamel) Lindl., Bot. Reg. 14: t. 1164. 1828. TYPE: We do not know whether a lectotype has ever been designated.

Deciduous small tree or large shrub to 6–10 m high; young twigs purple-brown or dark purple, 3–4 mm diam., sparsely to densely pubescent, or hairy only at the leaf axils, soon glabrescent; terminal winter buds ovoid, densely brownish villous with somewhat shiny hairs. Stipules densely pubescent with appressed, long, straight, and brownish hairs, adnate to the petiole, scars 4–15 mm long. Leaves membraneous to chartaceous, dark bright green, covered with scattered hairs everywhere or along midrib and nerves above, greenish, pubescent with long, straight, undulate to curly, colorless hairs along midrib, nerves and reticulation beneath, obovate, 6–17.5(–22) × 4–9(–13) cm; apex usually abruptly short-acuminate, acumen 3–20 mm long, base obtuse, cuneate to attenuate; nerves conspicuous below, in 7–10 pairs, reticulation coarsely netted, obscure on both surfaces. Petiole pubescent, 1–1.5 cm long. Flowers appearing before and after the leaves; peduncles densely pubescent with yellow to yellowish white hairs, 12–14 × 4–6 mm, pedicles 5–8 × 3–4 mm; tepals 9, white flushed with pink or purple outside, white or pink inside, spatulate to obovate, the outer 3 subequal to the inner 6 tepals, sometimes about half the length of the inner ones, 5–12.5(–15) × 2–5.5(–9) cm; stamens purple, 1–1.2(–1.4) cm long, anthers dehiscing laterally, connective appendage triangular, ca. 1 mm long, filaments 3–4 mm long; gynoecium green, glabrous to hairy, cylindric, 1.5–2.2 × 0.3–0.4 cm. Fruits cylindric, ca. 5–10 × 3 cm; ripe carpels ovoid to subglobose, white-lenticellate, 1–1.5 cm long, without beaks; torus with scars of perianth and stamens ca. 8 × 8 mm. Seeds broadly ovoid or obovoid, slightly compressed, ca. 1.2 cm long.

*Note.* Hybrid from *Magnolia heptapeta* and *Magnolia quinquepeta*, cultivated in gardens as an ornamental.

**Magnolia** (subgenus *Magnolia*) section **Theorhodon** Spach, Hist. Natur. Veget. Phanerog. 7: 470. 1839.

Stipules free from the petiole, leaves evergreen. Flowers neither precocious nor with a much reduced outer whorl of tepals, tepals subsimilar in texture. Fruit ellipsoid to oblong. Not native to China.

32. **Magnolia grandiflora** L., Syst. Nat. ed. 10 (2): 1082. 1759. TYPE: ?

Evergreen tree up to 30 m high in its original habitat; bark brownish or gray; young twigs stout, 6–7 mm diam., dull brown, densely yellowish sericeous, eventually glabrous. Stipules covered with the same indument as the young twigs, free from the petiole. Leaves thick coriaceous, dark green, glossy above, green, densely hairy with short to long, undulate to curly, colorless or brown hairs, gradually glabrescent beneath, elliptic, ovate to obovate, 10–20 × 4–10 cm; apex acute to short-acuminate, base cuneate to broadly cuneate; midrib and nerves visible on the undersides, nerves in 8–10 pairs, reticulation coarsely netted, prominent above, obscured below. Petiole 1.5–4 cm long, without stipular scars. Flowers erect, heavily scented, 15–20 cm diam., peduncles 3–4 × 0.8–0.9 cm, densely yellowish sericeous; pedicles very short, ca. 1 mm long; tepals 8–12, subsimilar, white, broadly obovate, broadly elliptic to orbicular, basally short-clawed, concave, thick fleshy, 8–10 × 5–8 cm; stamens purplish, ca. 2 cm long, anthers introrsely dehiscing, connective appendage triangular, ca. 2 mm long, filaments flat, 1–2 mm long; gynoecium ellipsoid, densely yellowish tomentose; carpels ovate, 1–1.5 cm, styles recurved. Fruiting peduncles 3–4 × 0.8–0.9 cm, pedicles ca. 1 mm long. Fruits ovoid-cylindric, 5–10 × 4–5 cm, densely brown or yellow tomentose; ripe carpels apically long-beaked, scars of perianth and stamens along torus 1.7–2 × 1 cm. Seeds ellipsoid to ovoid, compressed laterally, ca. 1.4 × 0.6 cm.

*Distribution.* Native of southeastern United States, cultivated in southern China.

*Uses.* Wood yellow-white, heavy and hard, used for interior finish; leaves, young shoots, and flowers extracted for volatile oil; the tree is a spectacular ornamental.

DUBIOUS NAMES

*Magnolia honanensis* B. C. Ding & T. B. Chao, J. Henan Agricultural College 4: 6. 1983. SYNTYPES: China. Henan: Yu Xian, *T. B. Chao et al. 838281, 838282* (in Herb. Henan College of Agriculture Conservatus) = *Magnolia biondii* Pamp.(?).

*Magnolia biondii* var. *parvialabastra* T. B. Chao, Y. H. Ren & J. T. Gao, J. Henan Agricultural College 4: 7. 1983. SYNTYPES: China. Henan: Nanchao Xian, *T. B. Chao et al. 83671, 83672* (in Herb. Henan College of Agriculture Conservatus) = *Magnolia biondii* Pamp.(?).

*Magnolia biondii* var. *ovata* T. B. Chao & T. X. Zhang, J. Henan Agricultural College, 4: 9. 1983. TYPE: China. Henan: Lushan Xian, *T. B. Chao et al. s.n.* (in Herb. Henan College of Agriculture Conservatus) = *Magnolia biondii* Pamp.(?).

*Magnolia biondii* var. *purpura* T. B. Chao & Y. C. Qiao, J. Henan Agricultural College, 4: 10. 1983. SYNTYPES: China. Henan: Lushan Xian, *Y. Z. Qiao et al. 0005, 0006* (in Herb. Henan College of Agriculture Conservatus) = *Magnolia biondii* Pamp.(?).

*Magnolia biondii* var. *planities* T. B. Chao & Y. Z. Qiao, J. Henan Agricultural College 4: 10. 1983. TYPE: China. Henan: Yu Xian, *T. B. Chao et al. s.n.* (in Herb. Henan College of Agriculture Conservatus) = *Magnolia biondii* Pamp.(?).

*Magnolia denudata* Desr. var. *pyramidalis* T. B. Chao & Z. X. Chen, J. Henan Agricultural College 4: 11. 1983. SYNTYPES: China. Henan: Zengzhou, *T. B. Chao et al. 83871, 83872* (in Herb. Henan College of Agriculture Conservatus) = *Magnolia heptapeta* (Buc'hoz) Dandy (?).

*Magnolia axilliflora* T. B. Chao, T. X. Zhang & J. T. Gao in T. B. Chao, Acta Agriculture Universitatis Henanensis 19(4): 360. 1985. SYNTYPES: China. Henan: Nanchao Xian, *T. B. Chao et al. 83815, 83816, T. X. Zhang et al. 82910, 82911* (in Herb. Henan College of Agriculture Conservatus) = *Magnolia biondii* Pamp.(?).

*Magnolia axilliflora* var. *alba* T. B. Chao, Y. H. Ren & J. T. Gao, Acta Agriculture Universitatis Henanensis, 19(4): 360, photo 4. 1985. SYNTYPES: China. Henan: *T. B. Chao, Y. H. Ren & S. D. Zhuao 855181, 855182, T. B. Chao, J. T. Gao et al. 854151, 854152* (flowering, in herb. Henan Agricultural University Conservatus) = *Magnolia biondii* Pamp.(?).

*Magnolia axilliflora* var. *multitepala* T. B. Chao, Y. H. Ren & J. T. Gao, Acta Agriculture Universitatis Henanensis, 19(4): 361. 1985.

SYNTYPES: China. Henan: *T. B. Chao, Y. H. Ren & S. D. Zhuao 855201, 85471* (flowering, in herb. Henan Agri. Univ.) = *Magnolia biondii* Pamp.(?).

*Magnolia funiushanensis* T. B. Chao, J. T. Gao & Y. H. Ren, Acta Agriculture Universitatis Henanensis, 19(4): 362, photo 5. 1985. TYPE: China. Henan: *T. B. Chao, J. T. Gao & Y. H. Ren 85019* (flowering, in herb. Henan Agri. Univ.) = *Magnolia biondii* Pamp.(?).

*Magnolia funiushanensis* var. *purpurea* T. B. Chao & J. T. Gao, Acta Agriculture Universitatis Henanensis, 19(4): 362. 1985. SYNTYPES: China. Henan: *T. B. Chao, et al. 855218, 855219* (flowering, in herb. Henan Agri. Univ.) = *Magnolia biondii* Pamp.(?).

*Magnolia biondii* var. *flava* T. B. Chao, J. T. Gao & Y. H. Ren, Acta Agriculture Universitatis Henanensis, 19(4): 362. 1985. SYNTYPES: China. Henan: *T. B. Chao, et al. 855207, 855208, 84019* (flowering, in herb. Henan Agri. Univ.) = *Magnolia biondii* Pamp.(?).

*Magnolia biondii* var. *tatitepala* T. B. Chao & J. T. Gao, Acta Agriculture Universitatis Henanensis, 19(4): 363. 1985. TYPE: China. Henan: *T. B. Chao & J. T. Gao 85472* (flowering, in herb. Henan Agri. Univ.) = *Magnolia biondii* Pamp.(?).

*Magnolia denudata* Desr. var. *angustitepala* T. B. Chao & Z. S. Chun, Acta Agriculture Universitatis Henanensis, 19(4): 363. 1985. SYNTYPES: China. Henan: *T. B. Chao, et al. 843151, 843512* (flowering, in herb. Henan Agr. Univ.) = *Magnolia heptapeta* (Buc'hoz) Dandy (?).

*Magnolia sinostellata* P. L. Chiu & Z. H. Chen, Acta Phytotax. Sin. 27, 1: 79. 1989. TYPE: China. Zhejiang: Caoyutang of Jingning, *J. P. Si & H. F. Pan JH-002* (holotype, HHBG; isotype, PE) = *Magnolia stellata (?)* (Siebold & Zucc.) Maxim.

**II. Manglietia** Blume, Verh. Bat. Gen. 9: 149. 1823. *Magnolia* sect. *Manglietia* (Blume) Baillon, Adansonia 7: 66. 1866. TYPE SPECIES: *Manglietia glauca* Blume.

*Paramanglietia* Hu & Cheng, Acta Phytotax. Sin. 1, 2: 255. 1951. TYPE SPECIES: *Paramanglietia aromatica* (Dandy) Hu & Cheng.

*Manglietiastrum* Law, Acta Phytotax. Sin. 11: 72, t. 2. 1979. TYPE SPECIES: *Manglietiastrum sinicum* Law.

*Tree.* Stipules adnate to or free from petiole. Flowers terminal, solitary, bisexual; tepals 9–13, 3-merous, subequal; anthers introrse, connective produced into a short or long appendage. Gynoecium sessile, but a gynophore present in section *Manglietiastrum*. Follicles free, crowded, dehiscent along the dorsal and sometimes also the ventral suture.

*Distribution.* About 25 species in tropical and subtropical Asia from the eastern Himalayas eastward to southern China and Malesia (not in the Moluccas and New Guinea). Eighteen species in China.

*Note.* *Manglietia* is still treated as a separate genus mainly because the number of ovules is 4–12(–16), while in *Magnolia* it is 2(–4). Leaf and wood anatomical characters point to the fact that *Manglietia* consists of a group of closely related species, although the similarity with *Magnolia* is great. However, all genera of Magnoliaceae as recognized by Nooteboom (1985) are quite similar in anatomical characters.

Many species of *Manglietia* have a hypodermis of 1–2 subepidermal layers beneath the upper epidermis, some also adjacent to the lower epidermis; few species have this hypodermis adjacent only to the lower epidermis. Species of *Magnolia* mostly lack a hypodermis. *Manglietia* consists entirely of evergreen species, thus the anatomy must be compared with the anatomy of evergreen species of *Magnolia*. The species of *Manglietia* usually do not have helical thickenings and usually have scalariform perforations and large vessel-ray pits throughout the rays; this pitting is present only in the marginal ray cells of the evergreen species of *Magnolia*. Scalariform perforations do occur in some deciduous species of *Magnolia*, and helical thickenings are found in a few species of *Manglietia*.

Regarding *Manglietia sinica* [*Manglietiastrum sinicum* Law, *Magnolia sinica* (Law) Noot.; Nooteboom (1985) at that time was not able to study any collections], we conclude that the number of ovules, as well as the sometimes well-developed hypodermis, and the scalariform and unilateral compound vessel-ray pitting throughout the rays, warrant regarding it as a species of *Manglietia*, not of *Magnolia*. Moreover, oil cells are usually absent in the rays, as in *Manglietia*. However, the discontinuous helical thickenings in the vessels point to *Magnolia*, although this character is found in a few other species of *Manglietia*.

KEY TO THE SPECIES OF *MANGLIETIA*
(primarily based on flower characters)

1. Twigs glabrous. ..... 2
1. Twigs hairy at least when young. ..... 12
2(1). Gynoecium stipitate; stipules free. ..... 18. *Manglietia sinica*

2. Gynoecium not stipitate; stipules adnate to petiole. ..... 3
3(2). Leaves glaucous beneath. ..... 4
3. Leaves not glaucous beneath. ..... 6
4(3). Twigs 4–5 mm thick; leaf base narrowly cuneate, reticulation rather obscure. ..... 2. *Manglietia conifera*
4. Twigs 6–10 mm thick; leaf base cuneate, reticulation distinct. ..... 5
5(4). Peduncle 15 mm long; stipules pubescent; leaves obovate, 5–7 cm broad, apex short-acuminate; gynoecium hairy; fruits ovoid, 6 cm long, follicles hairy. ..... 13. *Manglietia microtricha*
5. Peduncle 30–34 mm long; stipules glabrous; leaves narrowly obovate, 10.5–13 cm broad, apex acuminate; gynoecium glabrous; fruits ovoid-oblong, 10–16 cm long, follicles glabrous. ..... 8. *Manglietia grandis*
6(3). Peduncle 5–7 mm thick. ..... 7
6. Peduncle 2–4 mm thick. ..... 9
7(6). Leaves 11–16 cm broad, reticulation distinct; stipular scars on petiole 16–45 mm long; peduncle hairy; flower purple or red, outer tepals 12–14 cm long; gynoecium 27 mm high, carpels 70–80; fruits 9.5 cm long. ..... 11. *Manglietia lucida*
7. Leaves 3.5–10 cm broad, reticulation rather obscure; stipular scars on petiole 1–7 mm long; peduncle glabrous; flower (greenish) white, outer tepals 5.5–8(–20) cm long; gynoecium 16–22 mm high, carpels 12–30 or 38–46; fruits 5–7 cm long. ..... 8
8(7). Pedicle 4 mm; stipules (rufous) villous; leaf base cuneate; apex short-acuminate; petiole not dilated at base; outer tepals oblong; connective appendage of anthers semiorbicular, 1 mm long, filaments 1 mm long; gynoecium ovoid; fruiting peduncles 3–5.5 cm long, fruits ellipsoid. ..... 15. *Manglietia pachyphylla*
8. Pedicle 6–8 mm; stipules pubescent; leaf base attenuate-cuneate, apex acuminate; petiole dilated at base; outer tepals obovate-elliptic; connective appendage of anthers triangular, 1.8 mm long, filaments 2 mm long; gynoecium broadly ellipsoid; fruiting peduncles 9–11 mm long, fruits ovoid or ovoid-globose. ..... 5b. *Manglietia fordiana* var. *calcarea*
9(6). Carpels 45–86. ..... 10
9. Carpels (12–)20–36. ..... 11
10(9). Gynoecium glabrous, tree to 25 m high; stipules glabrous or pubescent; reticulation of leaf distinct; outer tepals thin-coriaceous, stamens 13–16 mm long, connective appendage triangular with a sharp pointed tip, filaments 2–5 mm long; gynoecium ovoid or narrowly ovoid, 17–28 mm high; fruiting peduncles 5–10 mm thick, fruits ovoid-oblong or cylindric, 6.5–11 cm long; scars of perianth and stamens along torus under fruit 14–20 mm long. ..... 10. *Manglietia insignis*
10. Gynoecium hairy, tree to 8 m high; stipules sparsely hairy; reticulation of leaf rather obscure; outer tepals thick-fleshy, stamens 10 mm long, connective appendage triangular, filaments 1 mm long; gynoecium ellipsoid, 14–15 mm high; fruiting peduncles 3–4 mm thick, fruits ovoid-ellipsoid, 3.5 cm long; scars of perianth and stamens along torus under fruit 7–9 mm long. ..... 4. *Manglietia duclouxii*
11(9). Outer tepals 5.5–7 cm long, inner tepals 4–4.8 cm long; connective appendage of anthers triangular, 1.8 mm long; leaf base cuneate, reticulation coarse. ..... 5a. *Manglietia fordiana* var. *fordiana*
11. Outer tepals 3.5 cm long, inner tepals 2.8 cm long; connective appendage of anthers semiorbicular, 1–1.5 mm long; leaf base narrowly cuneate, reticulation fine. ..... 2. *Manglietia conifera*
12(1). Leaves glaucous beneath. ..... 13
12. Leaves not glaucous beneath. ..... 15
13(12). Peduncle 10 mm long; apex of leaf short-acuminate, petiole dilated at base; outer tepals 2–2.2 cm long, thick-fleshy; connective appendage of anthers triangular. ..... 3. *Manglietia dandyi*
13. Peduncle 15–90 mm long; apex of leaf acuminate or acute, petiole not dilated at base; outer tepals 3.5–7.5 cm long, thin-coriaceous; connective appendage of anthers triangular with a sharp pointed tip, or semiorbicular. ..... 14
14(13). Stipules glabrous; reticulation of leaf distinct, coarse, base cuneate; pedicle present; inner tepals obovate or elliptic; connective appendage of anthers triangular with a sharp pointed tip, 4 mm long; scars of bracts 2 or 3. ..... 7. *Manglietia glauca* var. *sumatrana*
14. Stipules pubescent; reticulation of leaf rather obscure, fine, base narrowly cuneate; pedicle absent; inner tepals spathulate; connective appendage of anthers semiorbicular, 1–1.5 mm long; scars of bracts 0 or 1. ..... 2. *Manglietia conifera*
15(12). Carpels 20–39. ..... 16
15. Carpels 44–88. ..... 19
16(15). Outer tepals 3.5 cm long; flower (greenish) yellow or yellowish, inner tepals 2.8 cm long. ..... 2. *Manglietia conifera*
16. Outer tepals 5.5–8 cm long; flower (greenish) white, inner tepals 4–8 cm long. ..... 17
17(17). Connective appendage semiorbicular; inner tepals 9; gynoecium ellipsoid; fruits subglobose; scars of perianth and stamens along torus under fruit 7–10 mm long. ..... 1. *Manglietia aromatica*
17. Connective appendage triangular or very long, narrowly triangular; inner tepals 6 or 7; gynoecium ovoid; fruits ovoid; scars of perianth and stamens along torus under fruit 13–22 mm long. ..... 18
18(18). Connective appendage very long, narrowly triangular; reticulation of leaves distinct, petiole dilated at base; filaments 1 mm long. ..... 5c. *Manglietia fordiana* var. *forrestii*
18. Connective appendage triangular; reticulation of leaves rather obscure, petiole not dilated at base; filaments 1.5–2 mm long. ..... 5a. *Manglietia fordiana* var. *fordiana*

19(15). Leaves glabrous. ..... 20
19. Leaves hairy beneath at least when young. 22
20(19). Peduncle 30–37 mm long. ..... 9. *Manglietia hookeri*
20. Peduncle 10–15 mm long. ..... 21
21(20). Leaves 11–16 cm broad, obovate, reticulation coarse; peduncle stout, 6 mm thick; outer tepals 12–14 cm long, thick-fleshy; fruiting peduncles 4.5 cm long, fruits ovoid. ..... 11. *Manglietia lucida*
21. Leaves 4–8 cm broad, elliptic or narrowly obovate, reticulation fine; peduncle slender, 4 mm thick; outer tepals 5–7 cm long, thin-coriaceous; fruiting peduncles 1.2–2.5 cm long, fruits ovoid-oblong or cylindric. ..... 10. *Manglietia insignis*
22(19). Peduncle 10.1–13 mm thick. ..... 12. *Manglietia megaphylla*
22. Peduncle 4–10 mm thick. ..... 23
23(22). Peduncle 4.1–10 mm thick. ..... 24
23. Peduncle 4 mm thick. ..... 28
24(23). Twigs in innovations 5.1–12 mm thick. ..... 25
24. Twigs in innovations 2–5 mm thick. ..... 26
25(24). Pedicle absent; twigs pubescent, stipules pubescent; leaves minutely (scattered) hairy beneath, apex short-acuminate. ..... 6. *Manglietia garrettii*
25. Pedicle present; twigs villous, stipules (rufous) villous; young leaves with longer hairs beneath, apex acuminate or acute. ..... 12. *Manglietia megaphylla*
26(24). Gynoecium hairy; hairs white; follicles hairy. ..... 17. *Manglietia ventii*
26. Gynoecium glabrous; hairs brown or red, follicles glabrous. ..... 27
27(26). Gynoecium 13–15 mm high; twigs villous, 4–5 mm diam., stipules (rufous) villous; young leaves with longer hairs beneath, reticulation rather obscure, petiole not dilated at base; flower creamy white, outer tepals coriaceous, 3.7–5.7 × 2–2.5 cm, the inner petals 9–12 cm long; connective appendage short pointed or semiorbicular, 1–1.5 mm long, fruiting peduncles slender, fruits ovoid. ..... 14. *Manglietia moto*
27. Gynoecium 30 mm high; twigs pubescent, 5–8 mm diam., stipules pubescent; leaves minutely (scattered) hairy beneath, reticulation distinct, petiole dilated at base; flower purple or red, outer tepals thick-fleshy, 6–6.5 × 3 cm, the inner ones slightly smaller; connective appendage triangular, 3 mm long; fruiting peduncles stout, fruits ovoid-oblong. ..... 6. *Manglietia garrettii*
28(23). Peduncle (22–)31–90 mm long. ..... 29
28. Peduncle 10–30 mm long. ..... 30
29(28). Pedicle absent; twigs villous, stipules (rufous) villous; young leaves with longer hairs beneath; inner tepals 9–12 cm, outer tepals 3.7–5.7 cm long. ..... 14. *Manglietia moto*
29. Pedicle present; twigs pubescent, stipules pubescent; leaves minutely (scattered) hairy beneath; inner tepals 2.7–4.5 cm, outer tepals 4–4.5 cm long. ..... 5d. *Manglietia fordiana* var. *kwangtungensis*
30(28). Gynoecium hairy; pedicle absent; follicles hairy. ..... 17. *Manglietia ventii*
30. Gynoecium glabrous; pedicle present; follicles glabrous. ..... 31
31(30). Peduncle 10–15 mm long, pedicle 3–5 mm; reticulation of leaf distinct; outer tepals thin-coriaceous; connective appendage of anthers triangular with a sharp pointed tip, filaments 2–5 mm long; gynoecium 17–28 mm high; fruits ovoid-oblong or cylindric, 6.5–11 cm long; scars of perianth and stamens along torus under fruit 14–20 mm long. ..... 10. *Manglietia insignis*
31. Peduncle 22–30 mm long, pedicle 1–2 mm; reticulation of leaf rather obscure; outer tepals coriaceous; connective appendage of anthers semiorbicular, filaments 1 mm long; gynoecium 11–15 mm high; fruits ovoid, 2.5–3.5 cm long; scars of perianth and stamens along torus under fruit 9 mm long. ..... 5d. *Manglietia fordiana* var. *kwangtungensis*

## Key to the Species of *Manglietia*
(based primarily on fruit characters)

1. Stipules free; gynoecium stipitate. ..... 18. *Manglietia sinica*
1. Stipules adnate to petiole; gynoecium not stipitate. ..... 2
2(1). Follicles hairy. ..... 3
2. Follicles glabrous. ..... 7
3(2). Pedicle present; leaves narrowly elliptic or narrowly obovate. ..... 4
3. Pedicle absent; leaves elliptic or obovate. 5
4(3). Tree ca. 15 m high; twigs yellowish villous when young, 4–5 mm diam.; stipules pubescent; reticulation of leaf distinct; stipular scars 9–11 mm long; peduncle hairy; flower (greenish) white; outer tepals ovate or oblong; stamens 12–20 mm long; gynoecium 17–25 mm high. 16. *Manglietia szechuanica*
4. Treelet ca. 8 m high; twigs glabrous, 3 mm diam.; stipules sparsely hairy; reticulation of leaf rather obscure; stipular scars 2–3 mm long; peduncle glabrous; flower purple or red; outer tepals obovate; stamens 10 mm long; gynoecium 14–15 mm high. ..... 4. *Manglietia duclouxii*
5(3). Young twigs densely tomentellous, 2–3.5 mm thick; leaves not glaucous beneath. ..... 17. *Manglietia ventii*
5. Young twigs glabrous or rather long-hairy, 6–10 mm thick; leaves glaucous beneath. 6
6(5). Twigs glabrous; leaves glabrous, reticulation distinct, fine; petiole glabrous; peduncle glabrous, 15 mm long. ..... 13. *Manglietia microtricha*
6. Young twigs with rather long, undulate to curly, spreading rufous hairs; leaves pubescent beneath at least when young, reticulation rather obscure, coarse; petiole hairy; peduncle hairy, 10 mm long. ..... 3. *Manglietia dandyi*
7(2). Pedicle absent. ..... 8
7. Pedicle present. ..... 15
8(7). Fruiting peduncles 11–14 mm thick. ..... 9
8. Fruiting peduncles 2–9 mm thick. ..... 10
9(8). Twigs and stipules glabrous; leaves glaucous beneath, narrowly obovate, 10.5–13 cm

broad; petiole not dilated at base; fruits oblong-ovoid, 10–16 × 6–10 cm; scars of perianth and stamens along torus under fruit 15–17 mm long; peduncle 30–34 mm long, 13–14 mm thick; flower pink; carpels 95–110; scars of bracts 0. ..... 8. *Manglietia grandis*

9. Young twigs densely appressed-pubescent; stipules pubescent; leaves not glaucous beneath, obovate or narrowly ovate, 6–9.5 cm broad; petiole dilated at base; fruits subglobose to ovoid, 8–8.5 × 5.2 cm; scars of perianth and stamens along torus under fruit 7 mm long; peduncle 12–20 mm long, 4–5 mm thick; flower white; carpels 29–39; scars of bracts 1 or 2. ..... 1. *Manglietia aromatica*

10(8). Carpels 48–88. ..... 11

10. Carpels (12–)20–36. ..... 12

11(10). Young leaves scattered hairy with long, dark brown hairs beneath, 11–19 × 5–7 cm; twigs and stipules brown to rufous villous; apex acuminate or mucronate; reticulation rather obscure; petiole not dilated at base; fruits ovoid; flower (greenish) white or (greenish) yellow or yellowish; outer tepals coriaceous; connective appendage short-pointed or semiorbicular, 1–1.5 mm long; gynoecium 13–15 mm high. ..... 14. *Manglietia moto*

11. Leaves minutely brownish hairy beneath, 18–34.5 × 8–12 cm; twigs and stipules pubescent; apex short-acuminate; reticulation distinct; petiole dilated at base; fruits oblong; flower purple or red; outer tepals thick-fleshy; connective appendage triangular, 3 mm long; gynoecium 30 mm high. ..... 6. *Manglietia garrettii*

12(10). Fruiting peduncles 4.1–6 mm thick. ..... 13

12. Fruiting peduncles 2–4 mm thick. ..... 14

13(12). Leaves not glaucous, glabrous or minutely scattered hairy beneath; petiole not dilated at base, stipular scar 2–6 mm long; peduncle 4 mm thick; outer tepals 5.5–7 cm long, thin-coriaceous; inner tepals 4–4.8 cm long; connective appendage 1.8 mm long; filaments 1.5–2 mm long; scars of bracts 1. ..... 5a. *Manglietia fordiana* var. *fordiana*

13. Leaves glaucous, densely pubescent beneath when young; petiole dilated at base, stipular scar 6–10 mm long; peduncle 5 mm thick; outer tepals 2 2.2 cm long, thick-fleshy; inner tepals 1.8–2 cm long; connective appendage 1 mm long; filaments 1 mm long; scars of bracts 2. ..... 3. *Manglietia dandyi*

14(12). Twigs 4–10 mm diam., usually glabrous, sometimes pubescent at the annular scars; reticulation of leaf coarse, base cuneate; flower (greenish) white; outer tepals 5.5–7 cm long; inner tepals 4–4.8 cm long; connective appendage triangular, 1.8 mm long. ..... 5a. *Manglietia fordiana* var. *fordiana*

14. Twigs 4–5 mm diam., usually ferrugineous pubescent when young; reticulation of leaf fine, base narrowly cuneate; flower (greenish) yellow or yellowish; outer tepals 3.5 cm long; inner tepals 2.8 cm long; connective appendage semiorbicular, 1–1.5 mm long. ..... 2. *Manglietia conifera*

15(7). Fruits ovoid-globose, 9.5 × 8–10 cm or 7–9.5 × 6–8.5 cm. ..... 16

15. Fruits ovoid, ovoid-oblong, cylindric, ellipsoid, or oblong, 2.5–8 × 2.5–5.5 cm. ..... 18

16(15). Twigs glabrous to minutely hairy; fruiting peduncles 4.5 cm long; fruits 9.5 × 8–10 cm; stipules pubescent; leaves and petiole glabrous. ..... 11. *Manglietia lucida*

16. Twigs densely and longer hairy when young. 17

17(16). Leaves 23–40 × 9.4–17 cm; fruiting peduncles 10–30 × 10–13 mm; stipules (rufous) villous; leaves scattered villous with long undulate to curly dark brown hairs beneath at least when young; petiole hairy. ..... 12. *Manglietia megaphylla*

17. Leaves 21–32 × 6.5–10 cm; fruits 7–9.5 × 6–6.5 cm broad; peduncle 30–37 × 7–10 mm; pedicle 7–13 mm. ..... 9. *Manglietia hookeri*

18(15). Leaves glaucous beneath; fruit ovoid to ovoid-oblong, 3.5–8 × 2.5–5.5 cm; scars of bracts 2 or 3. ..... 7. *Manglietia glauca* var. *sumatrana*

18. Leaves not glaucous beneath; scars of bracts 0 or 1. ..... 19

19(18). Scars of perianth and stamens along torus under fruit 7–9 mm long. ..... 20

19. Scars of perianth and stamens along torus under fruit 12–22 mm long. ..... 21

20(19). Twigs hairy at least when young; fruit ovoid or irregular, 2.5–3.5 × 2.5 cm; tree of ca. 15 m high; stipules pubescent; petiole hairy; fruiting peduncles 3–3.5 cm long, 5 mm thick; peduncle hairy, 22–31 mm long; flower (greenish) white; outer tepals coriaceous; connective appendage semiorbicular, 1 mm long; gynoecium glabrous, ovoid; styles 1–1.5 mm long. ..... 5d. *Manglietia fordiana* var. *kwangtungensis*

20. Twigs glabrous; fruits ovoid-ellipsoid, ca. 3.5 cm long; treelet ca. 8 m high; stipules sparsely hairy; petiole and peduncle glabrous; fruiting peduncles 1.3–1.5 cm long, 3–4 mm thick; peduncle 13–15 mm long; flower purple or red; outer tepals thick-fleshy; connective appendage triangular, 2–3 mm long; gynoecium hairy, styles 3–4 mm long. ..... 4. *Manglietia duclouxii*

21(19). Fruits ovoid-oblong, cylindric, or ellipsoid, 5–7 × 4.5 or 6.5–11 × 3–4 cm; peduncle 10–20 mm long; pedicle 3–5 mm; connective appendage triangular with a sharp pointed tip or semiorbicular; twigs 3–8 or ca. 10 mm diam. ..... 22

21. Fruits ovoid-globose or irregular, 2.5–6 × 2–5 cm; connective appendage triangular or very long, narrowly triangular; twigs 3–8 mm diam. ..... 23

22(21). Fruits ellipsoid, 5–7 × 4.5 cm; stipules (rufous) villous; apex of leaf short-acuminate, reticulation rather obscure; peduncle stout, 7 mm thick; outer tepals coriaceous;

connective appendage semiorbicular; filaments 1 mm long. ..... 15. *Manglietia pachyphylla*

22. Young twigs glabrous or pubescent at the nodes, 3–8 mm diam.; fruits ovoid-oblong to ovoid-cylindric, sometimes irregular, 6.5–11 × 3–4 cm; stipules glabrous or pubescent; apex of leaf acuminate or mucronate, reticulation distinct; peduncle slender, 4 mm thick; outer tepals thin-coriaceous; connective appendage triangular with a sharp pointed tip; filaments 2–5 mm long. ..... 10. *Manglietia insignis*

23(21). Young twigs densely brown pubescent, 3–6 mm diam.; fruits ovoid, 4–5.5 × 3.5–5 cm; reticulation of leaf distinct; connective appendage very long, narrowly triangular; filaments 1 mm long. ..... 5c. *Manglietia fordiana* var. *forrestii*

23. Fruits ovoid to ovoid-globose or irregular, 2.5–6 × 2–5 cm; reticulation of leaf rather obscure; connective appendage triangular; filaments 1.5–2 mm long. ..... 24

24(23). Twigs glabrous, 5–7 mm diam.; base of leaf attenuate-cuneate; petiole dilated at base; peduncle 5–6 mm thick; pedicle 6–8 mm; gynoecium broadly ellipsoid, 16–20 mm high; scars of bracts 0. ..... 5b. *Manglietia fordiana* var. *calcarea*

24. Young twigs glabrous or pubescent at the nodes, 4–8 mm diam.; base of leaf cuneate; petiole not dilated at base; peduncle 4 mm thick; pedicle 0–1 mm; gynoecium ovoid, 13–15 mm high; scars of bracts 1. ..... 5a. *Manglietia fordiana* var. *fordiana*

## II-1. **Manglietia** section **Manglietia**

Gynoecium sessile. Stipules ± adnate to petiole, at least in China.

1. **Manglietia aromatica** Dandy, J. Bot. 69: 231. 1931. *Paramanglietia aromatica* (Dandy) Hu & Cheng, Acta Phytotax. Sin. I: 255. 1951. TYPE: *R. C. Ching 7421* (holotype, BM; isotypes, NY, PE). Figure 2.

Tree to 20 m high and 50 cm diam., bark gray; young twigs at first densely appressed-pubescent with short, straight, gray or brownish hairs, soon glabrescent, stout, 7–10 mm diam., black-brown, later gray-brown; terminal buds ovoid, densely hairy, 2–2.4 cm long; stipules densely appressed-pubescent with rather long, straight, yellowish hairs, adnate to the petiole. Leaves glabrous, thinly coriaceous to coriaceous, (narrowly) obovate, 17–22.5 × 6–9.4 cm; apex mucronate or acuminate, base cuneate; nerves in 9–16 pairs; midrib impressed above; reticulation coarse, prominent. Petiole glabrous, 2.7–3.5 cm long, conspicuously dilated toward the base, stipular scars 5–12 mm long. Peduncles glabrous, ca. 12 × 4–5 mm, pedicles absent. Flowers white, tepals 12, subequal, obovate to narrowly obovate, 6–8 × 2.5 cm, 3-merous; stamens 1–1.2 cm long, filaments 1–2 mm long, connective appendage semiorbicular; gynoecium ellipsoid, ca. 16 × 10 mm; scars of perianth and stamens on the torus 7–10 × 6–10 mm. Fruiting peduncle 13–20 × 11 mm. Fruits subglobose to ovoid, ca. 8–8.5 × 5.2 cm; torus with scars of perianth and stamens 0.7–2 × 1 cm; carpels 29–39, with thick and ligneous wall, free when ripe, their dorsal faces 10–25 × 0.8–1.9 cm, adaxial parts 1–2 cm long, dehiscing along the dorsal and ventral suture; fruiting peduncles stout, 1.3–1.9 × 0.6–1.2 cm. Seeds broadly ellipsoid, 10–12 × 7–8 mm.

*Distribution.* China and northern Vietnam. In CHINA. **Guangxi**: Bako Shan, Poseh, near Yunnan border, *Ching R.C. 7421*; Lingle, *Ling Le Exped. 32928*; Donglin, *Chang C.C. 11432*. **Guizhou**: *Huang D.F. 1651*. **Southeastern Yunnan**: Guangnan, *Wang C.W. 87854*; Shichou District, *Law Y.W. 4074*, *Wu C.A. 62- 37*; Mar-li-po, Hwang-jin-in, *Feng K.M. 13009*; Si-chour-hsien, Faa-doou, *11990*.

*Ecology.* In mixed forest. Altitude 1,300–1,900 m. Trees in the natural forest (Jingping of Yunnan) reach a height of 20.4 m and a diameter of 40 cm by the age of 54 years. Flowering May–June; fruiting September–October.

2. **Manglietia conifera** Dandy, J. Bot. 68: 205. 1930. TYPE: *Fleury in Chevalier 37817* (holotype, P; isotype, L). Figure 3.

*Manglietia chingii* Dandy, J. Bot. 69: 232. 1931. TYPE: *R. C. Ching 8390* (holotype, BM; isotypes, A, K, NY, PE).

*Manglietia tenuipes* Dandy, J. Bot. 69: 232. 1931. TYPE: *R. C. Ching 7117* (holotype, BM; isotype, NY).

*Manglietia glaucifolia* Law, Guihaia 4(4): 263. 1986. TYPE: China. Leishan, Guizhou: alt. 1,580 m, *C. P. Chien et al. 50689* (holotype, PE not seen).

*Manglietia ovoidea* Chang & B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 108. 1988. TYPE: *B. L. Chen Gs 86182* (holotype, SYS).

Tree to 28 m high and 55 cm diam., twigs black-brown and covered with many annular stipular scars, 4–5 mm diam., usually densely ferrugineously pubescent in innovations, soon glabrescent. Stipules pubescent, adnate to the base of the petiole. Leaves thinly coriaceous to coriaceous, dark glossy green, glabrous above, pale green to ± glaucous, glabrous, or sometimes appressed-brown-hairy when young, soon glabrescent, usually the

FIGURE 2. *Manglietia aromatica* Dandy.—1. Branch with deflorated flower.—2. Flower.—3. Flower, outer tepals removed.—4. Fruit. Based on *SYS 161520 = Chen Bao Liang 86 S 109*. Drawing by Xie Qing Jian.

hairs microscopically small and the leaves seemingly glabrous beneath; elliptic to (narrowly) obovate, 12.3–19.6 × 4.3–6.4 cm; apex acute to (shortly) acuminate, base narrowly cuneate; midrib sulcate above, elevated below; nerves in 12–14(–17) pairs, meeting in a looped intramarginal vein; reticulation fine, inconspicuous on both sides. Petiole pubescent, glabrescent, sulcate above, 1.2–

FIGURE 3. *Manglietia conifera* Dandy.—1. Fruiting branch.—2. Fruit. Based on *SYS 161743* = *Chen Bao Liang GS 86-182*. Drawing by Xie Qing Jian.

1.5 cm, stipular scars on petiole 3–7 mm long. Peduncle variable in length, 1.5–9 × 0.2–0.4 cm, erect or recurved, glabrous to ± pubescent, pedicle absent, bract single, spathaceous, pubescent, directly under the perianth. Tepals 9–11, the outer tepals 3, yellowish green to green, obovate, thinly coriaceous, ca. 3.5 × 2.4 cm, inner tepals 6–8, spathulate, fleshy, outside glabrous, yellowish with a flush of purple at the base, ca. 2.8 × 1.4 cm; stamens numerous with purple base, 9–11 mm, including 1–1.5-mm-long blunt connective appendage; gynoecium ovoid, ca. 1.5 cm, carpels 20–28, glabrous, slightly connate when young, styles glabrous, 1–2.5 mm long; ovules 3–11 in each carpel. Ripe fruits ovoid to globose, 3.2–5.4 × 2.8–4.2 cm, the surface of the torus foveolate because of the dense scars of the fallen stamens, deeply depressed, scars of perianth and stamens ca. 5–16 × 4–7 mm along the torus; fruiting peduncle 1.5–9 × 0.2–0.4 cm, the dorsal face of the carpels 16–22 × 7–9 mm, elliptic, opening along the dorsal suture only or both along dorsal and ventral suture. Seeds flat, subcordate, 7–9 × 6–8 mm.

*Distribution.* China and northern Vietnam. In CHINA. **Guangdong**: Luoding, *Wang P.S. 614*; Ruyuan, *Ko S.P. 52921*; Sunyi Tai to Fat Youk Chong Ping, *Ko S.P. 51777*; Kung Ping Shan, and Vicinity Taan Faan, Fang Cheng Dist., *Tsang W.T. 26813*. **Guangxi**: Na Pa, Sup Man Ta Shan, *Liang H.Y. 69538*; Yeo Mar Shan, *Ching R.C. 7117*; Me Kon, Seh Feng, Dar Shan, S Nanning, *Ching R.C. 8390*; Damiaoshan, *Chun S.H. 14206*. **Yunnan**: Maguang, *Chen B.L. 87 F 195*; Mengze, *Xu Y.C. 595*.

*Ecology.* Locally fairly common, in mixed evergreen forests, on sandshale hills. Altitude: 500–1,700 m. Flowering May–June; fruiting September–October.

*Uses.* Wood used for general construction work and furniture, bark used for medicine. Also grown as an ornamental.

*Note.* The specimens examined are uniform in all characters, but the variation in length of the peduncles is considerable. There are, however, intermediate forms.

We were not able to see the type of *Manglietia glaucifolia* Law. Fortunately, Law's original description gives enough information to enable us to recognize it. Consideration of the diagnostic characters and the geographic distribution leads to the conclusion that *Manglietia glaucifolia* belongs to *Manglietia conifera*.

3. **Manglietia dandyi** (Gagnep.) Dandy in Praglowski, World Pollen Spore Fl., 3 (Magnoliaceae): 5. 1974. *Magnolia dandyi* Gagnep., Notulae Syst. 8: 63. 1939. TYPE: *Poilane 20714* (holotype, P). Figure 4.

Tree to 15 m high, ca. 18 cm diam.; bark gray, quite rough; the indument with long, undulate to curly, spreading, rufous hairs; young twigs 6–7 mm diam., at first densely pubescent, finally glabrescent, old ones gray to brown-gray, ± pubescent to glabrous. Stipules densely pubescent, adnate to the petiole, scars 6–10 mm long. Leaves membraneous to thinly coriaceous, dark green, slightly pubescent, especially along the midrib above, glaucous, at first densely pubescent, sooner glabrescent beneath, obovate, elliptic to obovate-elliptic, 16–24 × 5–8.5 cm; apex short-acuminate, acumen 5–10 mm long, base cuneate to obtuse; midrib slightly impressed above, nerves obscure above, conspicuous below, in 8–13 pairs, reticulation laxly netted, not prominent on both sides. Petiole densely pubescent, dilatate toward the base, 1.2–2.3 cm long. Peduncle pubescent, ca. 1 × 0.5 cm, pedicle absent; bracts 2, densely pubescent outside. Flower bud ovoid; tepals 9–11, subequal, white to yellowish, the outer 3 fleshy, obovate-oblong, pubescent outside at the base, 2–2.2 × 1.5–1.7 cm, the inner tepals 6–8, obovate, glabrous, often abruptly constricted near the base, 1.8–2 × 0.9–1.6 cm; stamens numerous, sparsely pubescent outside, 5.5–7 mm long, connective appendage triangular, ca. 1 mm long, filaments ca. 1 mm long; gynoecium ovoid, 10–13 mm long, carpels 24–30, glabrous to pubescent, ovules 2–10; scars of perianth and stamens along torus ca. 6 mm long in flower. Fruiting peduncles 2–4.5 × 0.5 cm. Fruits ovoid to cylindric, 6–7.5 × 1.8–2.5 cm, entirely connate when young; mature carpels glabrous or ± pubescent, dorsal faces 1–1.6 cm long in upper and 2–3 cm long in lower carpels, dehiscing along the dorsal suture; scars of perianth and stamens ca. 1.3 × 0.5 cm. Seeds orange-red, 1–2 in each carpel.

*Distribution.* China, Laos, and Vietnam. In CHINA. **Guangdong** Huashuishan, *Zheng P. 22*; Ruyuan, *Chen B.L. 80115*; Ying-teh District, *Tse H. 695*; Huangtung, Yaoshan, *Sin S.S. 9966*; Lok Chong, *Tso C.L. 20508*; Lung T'au Mountain, near Iu, *C.C.C. To Kang Peng cs 12179*; Pan Ling Tsze, *Chun W.Y. 5860*. **Guangxi**: Cangwu Xian, *Chun S.H. 10140*; He Xian, *Chen L.C. 500183*. **Yunnan**: Marlipo, Sze-tai-po, *Feng K.M. 13960*; Menglun, *Chang H.T. 6342*, Si-chour-hsien, Faa-doou, *Feng K.M. 11771*; Wenshan, *Gao T.X. 5*; Xichou, *Zhu D.Q. 5*.

*Ecology.* In evergreen broad-leaved forest. Altitude: 1,450–2,000 m. Flowering April; fruiting September–October.

FIGURE 4. *Manglietia dandyi* (Gagnep.) Dandy.—1. Fruiting branch (*Feng 13960*, P).—2. Partly deflorated flower.—3. Stamen.—4. Outer petal.—5. Inner petal (*Poilane 20714*, P). Drawing by Joop Wessendorp, Rijksherbarium, Leiden.

*Collector's note.* Fruits orange-red, usually yellow-greenish tinged with a little red when mature and becoming brown when dry.

*Notes.* C. Y. Wu & W. T. Wang (1957) misidentified this species as *Manglietia rufibarbata* non Dandy (1928). The latter species is from Vietnam and has not been recorded for China. See also under *Manglietia moto*.

The species has some noteworthy characters. (1) The base of the lowest carpels is sometimes decurrent along the torus, so a short gynophore seemingly occurs. (2) Sometimes there are three ovules in the lowest carpels and two above the middle carpels, instead of more than four ovules as normal in *Manglietia*. (3) The carpels are from glabrous to hairy throughout the area of its dis-

tribution. The mature fruits as seen in the field often become greenish yellow instead of purple as is common in fruits of Magnoliaceae.

4. **Manglietia duclouxii** Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 33, t. 5A. 1905. *Magnolia duclouxii* (Finet & Gagnep.) Hu in Hu & Chun, Icon. Pl. Sin. 2: 18, t. 68S. 1929. TYPE: *Ducloux 2133* (lectotype, selected here, P).

Tree of ca. 8 m, young twigs slender, ca. 3 mm diam., glabrous, yellow-brown, gray-black later. Stipules sparsely hairy. Leaves thinly coriaceous to coriaceous, glabrous, dark green above, pale green, glabrous or scattered appressed-pubescent with fine, rather short, straight, brown hairs, with long colorless hairs along the margin and the midrib beneath, narrowly obovate to elliptic, 10.2–16 × 3–4 cm; apex acuminate, base cuneate; nerves fine in 9–11 pairs; reticulation netted, inconspicuous. Petiole glabrous, lengthwise grooved above, 1–1.2 cm long, with a stipular scar 2–3 mm long. Peduncle glabrous, 1.3–1.5 × 0.3–0.4 cm, bract 1, pedicle 2–3 mm long. Tepals 9, usually outer ones larger than inner ones, fleshy, purple or red, obovate to broadly obovate, 2.8–3.5 × 1.5–2.3 cm; stamens ca. 10 × 2 mm, including 2–3-mm-long connective appendage and 1-mm-long filaments; gynoecium ellipsoid, 1.4–1.5 × 0.7–0.8 cm, carpels 45–55, narrowly elliptic, ferrugineous-hairy, ca. 7–8 mm; styles glabrous, ca. 3–4 mm long; ovules ca. 5 in each carpel. Fruits ovoid-ellipsoid, ca. 3.5 cm long (not seen). Scars of perianth and stamens 7–9 × 3–4 mm.

*Distribution.* Vietnam and China. In CHINA. **Guangxi**: Longgui, *Li Y.K. 430*. **Sichuan**: Gu Lin Xian, *Qiao H.R. 1114*; Gulin, *Gulin Yiyao Gongsi 846*. **Yunnan**: Long ky, *Maire E.E. s.n.*; Malipo Xian, *KUN 76298*; Wenshan, *Feng K.M. 22369*.

*Ecology.* In evergreen forest. Altitude: 700–1,800 m. Flowering May–June; fruiting September–October.

*Note.* *Manglietia duclouxii* is easily recognized by its slender twigs, thin, small leaves, which are usually covered with minute, short, and rather long hairs beneath, and the pubescent gynoecium.

5. **Manglietia fordiana** Oliver in Hook., Icon. Pl. 10: t. 1953. 1891. *Magnolia fordiana* (Oliver) Hu, J. Arnold Arbor. 5: 228. 1924. TYPE: *C. Ford 90* (holotype, K).

*Paramanglietia microcarpa* Chang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 53. 1961. TYPE: *S. K. Lau 4246* (holotype, SYS; isotype, A).

*Manglietia hainanensis* Dandy, J. Bot. 68: 204. 1930. TYPE: *Tsang & Fung 656 in Herb. Lingn. Univ. 18190* (holotype, BM; isotypes, A, K, MO, NY).

*Manglietia yuyuanensis* Law, Bull. Bot. Res. (China) 5, 3: 125. 1985. TYPE: China. Zhejiang: Changhua Xian, alt. 1,000 m, *X. Y. Hoo 23326* (IBSC not seen).

5a **Manglietia fordiana** var. **fordiana**.

Tree to 30 m high and 1.5 m diam.; young twigs 4–8(–10) mm diam., yellow-brown to dark brown, usually glabrous, sometimes pubescent only along the annular scars of the stipules. Stipules usually ± pubescent with ferrugineous hairs, adnate to the base of petiole. Leaves thinly coriaceous to coriaceous, both sides glabrous or minutely scattered-pubescent beneath, narrowly obovate, obovate-elliptic to narrowly elliptic, 8–16(–20) × 2.5–5.4(–7) cm; apex mucronate to acuminate, base cuneate, sometimes slightly decurrent into the petiole; midrib impressed above, elevated and glabrous or hairy below, nerves in 8–12(–17) pairs, reticulation coarse, hardly visible. Petiole glabrous or pubescent, sulcate on the upper side, 1.4–4.2 cm long, stipular scar glabrous or pubescent, 2–6 mm long. Peduncles glabrous or ferrugineous-pubescent, 8–13 × 4 mm, pedicles absent or to 1 cm long; bracts 1–2. Tepals 9, the outer 3 slightly larger than the inner ones, the tepals concave, thinly coriaceous, obovate-elliptic, greenish outside, hardly pubescent outside at the base, 5.5–7 × 2.5–4 cm, the inner tepals pure white, fleshy, spathulate to broadly obovate, with cuneate to short-clawed base, 4–4.8 × 1.5–2.2 cm; stamens numerous, 9–12 mm long, connective appendage short triangular, ca. 1.8 mm long, filaments glabrous, 1.5–2 mm long; gynoecium ovoid to subglobose, glabrous and smooth, 1.3–1.5 × 1–1.2 cm, carpels (12–)24–36, styles glabrous, 0.5–1 mm long. Fruits ovoid or sometimes irregular-shaped because the carpels are partly abortive, 2.5–6 × 2–3.5(–5) cm; fruiting peduncle 1–2.5 × 0.4–0.6 cm, pedicle 1–5(–9) mm long; ripe carpels sometimes only 4–10, torus with scars of perianth and stamens 1.3–1.7 × 0.4–0.5 cm. Seeds flat-ovate, ellipsoid or irregularly shaped, 6–10 × 4–7 mm.

*Distribution.* China and Vietnam. In CHINA. **Anhui**: Wangshan, *Cheng W.C. 4030*. **Fujian**: *Chung H.H. 2940*. **Guangdong**: Loh Fian mountain, *Funkhouser W.L. C.C.C. 9082 a*; Lok Chong, *Tso C.L. 21005*; Luh Fau Mountain, *Merrill E.D. 10904*; Ruyuan, *Chen*

*B.L. 315*; Sunyi Dist., *Wang C. 31135*; Tsengshing District, Naam Kwan Shan, *Tsang W.T. 20440*. **Guangxi**: Cangwu Xian, *Chun S.H. 10035*; He Xian, *Li Y.K. 401535*; Lungnan Xian, *Lau S.K. 4850*; Pingnan, *Wang C. 39230*. **Hainan**: Bak Sa, *Lau S.K. 25956*; Dai Land Dungta, *Chun N.K. & C.L. Tso 43956*; Dung Ka to Wen Fa Shi, *Chun N.K. & C.L. Tso 43687*; Fan ya to Yik Tsok Mau, *McClure F.A. C.C.C. 9652*; Jianfong, *Chang H.T. 6095*. **Zhejiang**: King Yuan, *Ching R.C. 2472*. HONG KONG. **Tai Mo Shan:** *Chan K.Y. 1033*; Ma On Shan, *Hu S.Y. 10169 A*. Also in Yunnan, Guizhou, Jiangzi, Hunan.

*Ecology.* In subtropical evergreen broad-leaved forest; usually the trees grow on granite and sandshale. It was reported that this tree was easily cultivated and grew fast. It had attained a height of 18 m and a diameter of ca. 23 cm after 28 years at Xinyi Xian in Guangdong Province. Altitude: 500–1,300 m. Flowering April–May; fruiting August–October.

*Uses.* Because of the nicely structured and medium-hard wood, the timber is used for house building, veneer, furniture, and musical instruments. The local people in Guangxi treat dry cough and constipation with the bark. The tree is also cultivated as an ornamental.

*Collector's note.* The bark is brownish gray, smooth; branches are dark gray; leaves are glossy dark green above and pale green below; the flower buds are solitary, terminal, ovoid, flowers are creamy white, fragrant, anthers red; young fruits are purplish; seed coat is orange.

*Note.* *Manglietia hainanensis* is conspecific with *Manglietia fordiana*. It differs from the latter only in the length of the pedicle and the texture of the leaves. Although the pedicle usually is absent in *Manglietia hainanensis*, it sometimes occurs and then varies in length from 0 to 5 mm, occcasionally to 7–9 mm (*H. Y. Liang 62608*) throughout its geographical range. The leaves of *Manglietia hainanensis* are generally thinner than those of *Manglietia fordiana*. This difference is not a reliable character, however, because the leaves of *Manglietia fordiana* show a continuous variation in texture. Thus, there is no character left to distinguish *Manglietia hainanensis* from *Manglietia fordiana*. Regarding *Manglietia yuyuanensis*, there is no doubt that it is conspecific with *Manglietia fordiana*, despite its glabrous leaves. The degree of hairiness varies in *Manglietia fordiana*, too. *Manglietia yuyuanensis* represents an extreme, glabrous form. *Manglietia fordiana* and all synonyms mentioned above possess a leaf hypodermis with sinuous anticlinal walls and ± subglobose to ovoid sclereids, not known in other species of *Manglietia* in China. *Manglietia globosa* and *Paramanglietia microcarpa* are easily recognizable as *Manglietia fordiana*.

5b. **Manglietia fordiana** var. **calcarea** (X. H. Song) B. L. Chen & Nooteboom, stat. nov. *Manglietia calcarea* X. H. Song, J. Nanjing Inst. Forest. 4: 46. 1984. TYPE: China. Guizhou: Mogan, Libo Xian, alt. 670 m, *X. H. Song & F. Gao 640* (NF not seen).

Tree to 14 m high and 35 cm diam.; young twigs 5–7 mm diam.; plant entirely glabrous except for the stipules. Stipules densely pubescent with straight, appressed, brown hairs, adnate to the very base of the petiole, scars 4–5 mm long. Leaves coriaceous, rigid, dark green above, obovate-elliptic to narrowly obovate, 14.5–20 × 3.5–7 cm; apex rounded with an acumen 6–10(–14) mm long, base attenuate-cuneate; midrib impressed above, elevated beneath, nerves obscure above, visible to hardly prominent below, in 14–17 pairs. Petiole 2.8–3.8 cm long, dilatate toward the base. Peduncle 5–8(–20) × 5–6 mm, pedicle 6–8 mm long. Tepals 9, white, the outer 3 obovate-elliptic, ca. 6.2 × 2.5 cm, apex rounded, the inner tepals spathulate, 4.5–5.5(–6) cm long; stamens many, 1.2 cm long, connective appendage triangular, ca. 1.8 mm long, filaments ca. 2 mm long; gynoecium broadly ellipsoid, ca. 1.6–2 × 1 cm, carpels 12–16(–30), ovules ca. 7; torus with the scars of perianth and stamens 8–14 × 5–6 mm. Fruiting peduncle ca. 9–11 × 6 mm. Fruit ovoid to ovoid-globose, ca. 6 × 5 cm, ripe carpels ligneous, dorsal face elliptic, dehiscing along the dorsal venture; scars of perianth and stamens 1.2–1.3 × 0.7–0.8 cm. Seeds oblong, 8–10 × 5–6 mm, 2–5 in each carpel.

*Distribution.* CHINA. **Guizhou**: Pinfa, *Cavalerie J. 3182*; Yunnan-sen District, *Cavalerie J. 2263*.

*Ecology.* In margin of forest, growing on limestone. Altitude: 600–800 m. Flowering April–May; fruiting August–September.

*Uses.* Good timber, beautiful flowers; the tree also cultivated as an ornamental.

*Note.* This variety is characterized by both twigs and leaves being glabrous, the gynoecium broadly ellipsoid, and the carpels narrowly elliptic.

5c. **Manglietia fordiana** var. **forrestii** (W. W. Smith ex Dandy) B. L. Chen & Noot., stat. nov. *Manglietia forrestii* W. W. Smith ex Dandy, Notes Roy. Bot. Gard. Edinburgh 16:

126. 1928. TYPE: *G. Forrest 26705 A* (holotype, E; isotypes, A, K, NY).

*Manglietia globosa* Chang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 53. 1961. TYPE: *R. C. Ching 8394* (holotype, SYS; isotype, NY).

Tree to 18 m high, 46 cm diam.; stipules, young twigs, petiole, peduncles, and outer tepals outside at the base densely brown-pubescent with short to long, straight, appressed hairs; young twigs brownish, 3–6 mm diam., old ones dull brown, gray pubescent with straight to curly hairs; leaves and midrib scattered-pubescent with short, straight hairs beneath. Stipules adnate to the base of the petiole. Leaves coriaceous, bright green, glabrous above, pale green below, usually obovate, rarely narrowly obovate, 13–24.5 × 5.4–9.6 cm; apex mucronate to abruptly acuminate, acumen 5–17 mm long, base cuneate; nerves fine, in 9–14 pairs; reticulation distinct beneath, fine or coarse. Petiole sulcate on upper face, dilated toward the base, 1.5–2.6 cm long, stipular scars 2–8 mm long. Peduncles stout, 1.4–2.6 × 0.4–1 cm, pedicles 2–5 mm long. Flowers pure white, fragrant; tepals 9(–10), outer 3 thinly coriaceous, obovate to oblong-obovate, brown-pubescent outside at the base, 6.3–7 × 3.4–4.8 cm, the inner tepals 6, fleshy, spathulate, obovate to ± subcircular, clawed at the base, 4–5.3 × 2–3.5 cm; stamens 1–1.5 cm long, connective appendage obtuse, filaments ca. 1 mm long; gynoecium ovoid, smooth, 1.2–2.2 × 1–1.4 cm, carpels 26–28, styles 1–2 mm long. Fruiting peduncles, 1.7–2.6 × 0.6–1 cm, pedicles 2–8 mm long. Fruits ovoid, 4–5.5 × 3.5–5 cm, dorsal faces of carpels 1.5–2 cm long in the upper to 3.5–4 cm long in the lower carpels, carpels densely papilliferous, with short beak, dehiscing along dorsal and ventral suture; torus with scars of perianth and stamens 1.3–2.2 × 0.5–0.9 cm.

*Distribution.* China and Annam. In CHINA. **Southwestern Guangxi**: Chu Fang Shan, 30 Li S W of Shan Fang, *Wang C.W. 39301, Ching R.C. 5910.* **Southern Yunnan**: Cangyuan, *Li S.P. Mu 199*; hills NW of Tengyueh, *Forrest G. 27300*; Nan-Chiao, *Wang C.W. 73474*; Szemeo, *Forrest G. 11988*; Pingpien, *Feng K.M. 5193*; Si-chour-hsien, Ting-mann, *12254.*

*Ecology.* In mixed broad-leaved or deciduous forests. Altitude: 540–2,400 m. Flowering June; fruiting September–October.

*Collector's notes.* Widely branched; flowers green-white or pure soft white, fleshy, fragrant, anthers purple; fruits creamy reddish.

*Uses.* The timber is used for doors, windows, and furniture.

*Note.* This variety differs from variety *fordiana* in young twigs, stipules, undersides of the leaves, petioles, peduncles, and the outer tepals outside at the base being brown pubescent; the leaves are larger, to 24.5 cm long and 9.6 cm wide.

5d. **Manglietia fordiana** var. **kwangtungensis** (Merr.) B. L. Chen & Nooteboom, stat. nov. *Manglietia kwangtungensis* (Merr.) Dandy, Kew Bull. 1927: 264. 1927. *Magnolia kwangtungensis* Merr., J. Arnold Arbor. 8: 5. 1927. TYPE: *K. P. To, W. T. Tsang & U. K. Tsang 345 in C. C. C. 12344* (holotype; A; isotypes, BM, E, MO, SYS, UC).

Tree 15 m high; young twigs, stipules, midrib beneath, petiole and peduncles densely pubescent with short to long, straight to undulate, rufous hairs; young twigs 4–5 mm diam. Leaves dark green glossy above, pale green, scattered appressed-pubescent with short, straight, rufous hairs below, coriaceous, (narrowly) obovate, 14.4–19 × 3.2–6.4 cm; apex (shortly) acuminate, base narrowly cuneate to cuneate; nerves fine in 9–13 pairs, reticulation inconspicuous on both sides. Petiole sulcate above, 1.3–2.2 cm long, stipular scars 3–5 mm long. Peduncles 2.2–3.1 × 0.4 cm, with only one bract scar near the base of perianth, pedicle 1–2 mm long. Tepals 9, the outer 3 obovate-oblong, coriaceous, greenish with a flush of purple, ± brown hairy outside at base, 4–4.5 × 2–2.5 cm, the inner tepals 6, white, spathulate to obovate, short-clawed at base, thick, fleshy, 2.7–4.5 × 0.9–2.3 cm; stamens 0.7–1.5 cm long, connective appendage blunt, ca. 1 mm long, filaments glabrous, ca. 1 mm long; gynoecium broadly ovoid, 1.1–1.5 × 0.9–1.1 cm, carpels 44–49, styles 1–1.5 mm long, scars of perianth and stamens along the torus 0.9–1.2 × 0.4 cm. Fruits ovoid to irregularly shaped because partly abortive, 2.5–3.5 × 2.5 cm; fruiting peduncles 3–3.5 × 0.5 cm, pedicles ca. 5 mm long; ripe carpels 7–10 mm long.

*Distribution.* CHINA. **Guangdong**: Ruyuan, Yingde, *C.C.C. 12344.* **Guangxi**: Damiaoshan, *Chen T.C. 617.*

*Ecology.* In mixed forest. Altitude: 700–1,000 m. Flowering May–June.

*Note.* Because of its rufous or red-brown indumentum, it is not too difficult to distinguish *Manglietia fordiana* var. *kwangtungensis* from varieties *fordiana* and *forrestii.* In addition, variety

*kwangtungensis* shows smaller flowers and many more carpels.

The collection *C.C.C. 12179*, cited under *Magnolia kwangtungensis* Merr. (1927), belongs to *Manglietia dandyi* (Gagnep.) Dandy.

6. **Manglietia garrettii** Craib, Kew Bull. 1922: 166. 1922. TYPE: *Garrett 114* (holotype, UT; isotypes, BM, K).

Tree to 20 m high and 1.2 m diam. Young twigs, stipules, petioles and peduncles densely brown pubescent with short to long, straight to slightly undulate hairs. Twigs brown, stout, 5–8 mm diam. Stipules adnate to the petioles, scars 1.8–2.5 cm long. Leaves densely coated with minute (even with hand lens hardly visible), brownish hairs beneath, coriaceous, (narrowly) elliptic to obovate, 18–34.5 × 8–12 cm; apex short-acuminate, base cuneate or rounded; nerves in 12–21 pairs, prominently elevated beneath, reticulation prominent on both sides, coarse; petiole 3–5 cm long, thickened toward the base. Peduncle 1.5–4 cm × 6–9 mm, pedicle absent. Flower buds elongate, 6–6.5 × 2.2–2.5 cm. Tepals 9, purple or violet-red, thick and succulent, 3 outer ones 6–6.5 × 3 cm, 6 inner ones slightly smaller; stamens 1.1–1.5 cm long, connective appendage triangular, ca. 3 mm long; gynoecium glabrous, ovoid to narrowly ovoid, ca. 3 × 2 cm, carpels 66–88; styles glabrous, 2–3 mm long. Fruits broadly ovoid-oblong, 4–9 × 3.5–6 cm; dorsal faces of ripe carpels 1–2 cm long in upper and 2.5–3.2 cm long in lower carpels, short-beaked. Scars of perianth and stamens 10–12 × 9 mm. Seeds ellipsoid, obovoid, and irregularly shaped, 9–14 × 5–8 mm.

*Distribution.* China (southern Yunnan), Thailand, and Vietnam.

7. **Manglietia glauca** Blume var. **sumatrana** (Miq.) Dandy, Kew Bull. 1928: 188. 1928. *Manglietia sumatrana* Miq., Fl. Ned. Ind. Suppl.: 367. 1861. TYPE: *Tijsmann 468* (holotype, L; isotype, BO).

*Manglietia pilosa* P. Parm., Bull. Sci. France Belgique 27: 217, 292. 1895. *Manglietia singalanensis* Agostini, Atti Com. Accad. Fisiocrit. Siena 9 (7): 22. 1926. TYPE: *Beccari PS 334* (holotype, FI; isotype, L).

Tree to 26 m high and 80–100 cm diam.; bark gray-brown; twigs green, 5–6 mm diam., appressed short-hairy. Stipules glabrous or with some hairs on the apex, adnate to the very base of the petiole. Leaves appressed-puberulent, with short to long, straight, colorless to brownish hairs, glaucous beneath, thinly coriaceous, obovate to narrowly obovate or narrowly elliptic, 10–35 × 3.5–12 cm; apex acuminate, acumen 3–15 mm long, base cuneate; nerves in 10–16 pairs, prominent below, reticulations laxly netted, visible on both sides. Petiole covered with the same indumentum as twigs, lengthwise shallowly grooved, 1.5–3 cm long, stipular scars never over ⅓ of the length of the petiole. Peduncles minutely pubescent only at the nodes, 1.5–4 cm long, pedicles 2–8 mm long. Flowers white, the outer 3 tepals thinly coriaceous, obovate-elliptic, greenish outside, 5–7.5 × 2–3 cm, the inner 6 tepals smaller than the outer ones; stamens numerous, 0.6–1.3 cm long, connective appendage very acute, ca. 4 mm long, filaments ca. 3 mm long; gynoecium ovoid to orbicular, ca. 15 × 7 mm, carpels 20–50. Fruits ovoid to ovoid-oblong, 3.5–8 × 2.5–5.5 cm; the carpels opening ventrally and then dorsally, after staying closed toward the basal side of the dorsal suture. Seeds flat-orbicular to ellipsoidal, often irregularly shaped, 5–8 × 4–5 mm.

*Distribution.* Native of Indonesia (western Sumatra), cultivated in Guangdong, Guangsi, and Fujien.

*Ecology.* In forests. Altitude 600–1,300 m (in Indonesia). Flowering February–April; fruiting September–October (in China).

*Uses.* Cultivated as an ornamental tree.

*Note.* Y. W. Law in W. C. Cheng (1983) and L. G. Lin (1985) treated this variety as *Manglietia glauca* Blume.

8. **Manglietia grandis** Hu & Cheng, Acta Phytotax. Sin. 1: 158. 1951. TYPE: *C. W. Wang 87020* (holotype, PE). Figure 5.

Tree 12 m high and 35 cm diam.; plant glabrous except the sometimes puberulent undersides of leaves; young twigs stout, 8–10 mm diam., usually covered with a waxy substance, so seemingly gray; stipules adnate to the base of the petioles. Leaves glabrous, glossy above, glaucous, glabrous or minutely scattered-puberulent, ± papilliferous beneath, coriaceous, narrowly obovate, 20–35.5 × 10.5–13 cm; apex acuminate, base cuneate; nerves 17–26 pairs, reticulation visible when dry. Petiole 2.6–4 cm long, stipular scars 5–8 mm long. Flower pink. Fruiting peduncle 3–3.4 × 1.3–1.4 cm, pedicle absent. Fruit oblong-ovoid, 10–16 × 6–10 cm; carpels 97–106, 3–4 cm, dehiscing along the dorsal and the ventral suture, beaks sharp and slightly recurved, 3–4 mm long. Scars of perianth and stamens along the torus 1.5–1.7 cm long.

FIGURE 5. *Manglietia grandis* Hu & Cheng.—1. Branch with flower bud.—2. Bud with bracts.—3. Fruit, one follicle enlarged. Based on *SYS 161411* = *Chen Bao Liang 86 S 297*. Drawing by Xie Qing Jian.

*Distribution.* CHINA. **Southeastern Yunnan**: Mar Li Po, *Wang C.W. 87020*.

*Ecology.* In subtropical forests, on sandy soil and limestone. Altitude: 800–1,800 m.

*Uses.* Wood straight-grained, fine-textured, very good for house building and furniture because of its durability.

*Note.* *Manglietia grandis* differs from other species by its much larger leaves, numerous car-

pels, and bigger fruits; the fruits are the largest in Chinese Manglietias so far as we know. We have not seen the mature flowers and therefore cannot describe them in detail.

9. **Manglietia hookeri** Cubitt & W. W. Smith, Records Bot. Surv. India 4: 273. 1913. *Magnolia hookeri* (Cubitt & W. W. Smith) Raju & Nayar, Indian J. Bot. 3, 2: 170. 1980. SYNTYPES: Silum and other stations in the Bhamo division of Upper Burma: *Cubitt 302A, 327* (CAL not seen), *Rodgers 314* (CAL).

Tree to 25 m high, 90 cm diam.; young twigs, stipules, petiole, and peduncles covered with an indument of straight, white, silver, to brownish appressed hairs. Twigs brown, stout, (4–)8–12 mm diam. Stipules adnate to the base of the petiole. Leaves glabrous on both sides, coriaceous, narrowly obovate (or elliptic), 21–32 × 6.5–10 cm; apex acuminate, base cuneate, ± decurrent along the petiole; nerves in 12–19 pairs, reticulation prominent when dry. Petiole conspicuously sulcate above, 2–3.5 cm long, stipular scar obvious, nearly to the base of the blade, usually 1.2–2 cm long. Peduncles stout, 1.5–3.7 × 0.5–0.7 cm, pedicles 0.7–1.3 cm long. Flowers white, ca. 10 cm diam.; tepals 9–12, the outer 3 thinly coriaceous, obovate, 7–10 × 3.5–4 cm, creamy above the middle, becoming greenish toward the base, the inner tepals 6–9, thick, fleshy, spathulate to obovate, 7–8.5 × 3–3.5 cm, narrowly and short-clawed at base; stamens 1.7–2.2 mm long, connective appendage triangular with a sharp-pointed tip, 1–2 mm long, filaments 3–5 mm long. Gynoecium ovoid to broad-ellipsoid, 1.8–2.3 × 1.3–1.5 cm; carpels 50–64, reddish brown when dry, styles black-brown, 4–7 mm long. Scars of fallen perianth and stamens 1.6–2 × 0.6–0.7 cm. Fruiting peduncles 1.7–4 × 0.7–1 cm, pedicles 0.9–1.5 cm long. Fruits ovoid to subglobose, 7–9.5 × 6–6.5 cm; dorsal face of the ripe carpels from 1–1.3 cm long in the upper to 2.3–3 cm long in the lower carpels, short-beaked, smooth, dehiscing dorsally. Seeds ovate, elliptic-ovoid, elliptic to irregularly shaped, 8–13 × 5–7 mm.

*Distribution.* China and Upper Burma. In CHINA. **Guizhou**: Wangmo Xian, *Zhang Z.S. 1395*. **Southwestern Yunnan**: Shweli-Salwin divide, *Forrest G. 15952*; Chen-Kang Hsien, *Wang C.W. 72797*; Hills 3 days S of Tengyueh, 24°40′N, 98°30′E, *Forrest G. 27364*; Jingdong, *Li M.K. 3515*; Menghai, *Li Y.H. 4068*; Tungkwong valley, 25°5′N, *Forrest G. 7725*; Shuning, *Yu T.T. 16559*; Tengchong, *Li W.Z. 8271*.

*Ecology.* In mixed forests. Altitude: 1,000–3,000 m. Flowering April–May; fruiting October.

*Collector's note.* The flower buds green, flowers white, purple-white, deep pink fleshy; fruit follicles conelike, green or black.

10. **Manglietia insignis** (Wall.) Blume, Fl. Javae: Magnol. 22. 1828. *Magnolia insignis* Wall., Tent. Fl. Nepal.: 3, t. 1. 1824. TYPE: *Wallich 973* (holotype, K; isotypes, BM, GH).

*Magnolia shanpaensis* Hu, Acta Phytotax. Sin. 1: 157. 1951. TYPE: *H. T. Tsai 56560*, p.p. (holotype, PE; isotype, A).

*Manglietia yunnanensis* Hu, Acta Phytotax. Sin. 1: 159. 1951. TYPE: *H. T. Tsai 56560*, p.p. (holotype, PE).

*Manglietia patungensis* Hu, Acta Phytotax. Sin. 1: 335. 1951. TYPE: *H. C. Chow 484* (holotype, PE; isotypes, A, E, NY).

*Manglietia maguanica* Chang & B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 109. 1988. TYPE *B. L. Chen & Y. H. Su 86 S 053* (holotype, SYS).

*Manglietia tenuifolia* Chang & B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 110. 1988. TYPE *B. L. Chen & Li 86 S 195* (holotype, SYS).

Tree to 25 m high and 50 cm diam.; young twigs glabrous or ferrugineous to yellowish pubescent at the node, usually 3–8 mm diam. Stipules glabrous, sometimes pubescent, adnate to the base of the petiole, 19–27 mm long. Leaves thinly coriaceous to coriaceous, shining green above, pale green, glabrous to minutely pubescent beneath, narrowly obovate to elliptic, 14.5–26.5(–30) × 4.3–7.8 cm; apex acuminate to mucronate, acumen 5–15 mm long; base cuneate, ± attenuate along the petiole; nerves fine, in 10–22 pairs, reticulation densely netted, prominent on both surfaces. Petiole sulcate above, 1.7–3.5 cm long, stipular scars glabrous or sometimes scattered-hairy, 4–10(–13) mm long. Peduncles glabrous to pubescent only near the scar of the fallen bract, 1–1.5 × 0.4 cm, pedicles 3–5 mm long. Flowers fragrant, tepals 9–12, the outer 3 obovate-oblong, 5–7 × 2–2.5 cm, thinly coriaceous, brown-greenish, sometimes white-hairy outside at the base, reflexed later, the inner 6–9 white to purple, spathulate to narrowly obovate, short-clawed at base, 5–6.5 × 1.3–2.5 cm; stamens 1.3–1.6 cm long, connective appendage triangular with a sharply pointed tip, 1–2 mm long, filaments glabrous, 2–5 mm long; gynoecium ovoid to ovoid-cylindric, 1.7–2.8 × 1–1.2 cm, carpels 50–86, glabrous, styles glabrous, 2–4 mm long. Fruiting peduncles 1.2–2.5 × 0.5–1 cm, pedicles 0.5–1.1 cm long. Fruits ovoid-oblong, sometimes irregularly shaped because part of carpels abortive, 6.5–11 × 3–4 cm, the scars of perianth and stamens along the torus 1.4–2 × 0.6–0.7 cm; ripe carpels 0.7–1.2

cm long in the upper and 1–2 cm long in the lower carpels, dehiscing along the dorsal suture, obviously papilliferous, apex short-beaked.

*Distribution.* Nepal, northeastern India, China, northern Burma, northern Vietnam. In CHINA. **Guangxi**: Damiaoshan, *Chun S.H. 15857*; He Xian, *Chen Z.Z. 52125*; Lingui, *51153*; Longsheng, *51134*; Quan Xian, *Tsoong C.H. 81657*. **Guizhou**: Kaili Xian, *Qiannan Exped. 2081*; In silva frondosa collis ad vic. Yudong, *Hand.-Mazz. 2099*. **Hunan**: Xinning Ziyushan, *Li Z.Y. 56*; Chengbu, *Cao T.M. 830703*; Yongshun, *Hunan Exped. 387*. **Hubei**: Patung Hsien, *Chow H.C. 484*. **Sichuan**: Jiangjin Xian, *Chen S.J. 840092*; Kuan-hsien, *Liu Y.S. 1401*; Miyi Xian, *Wu S.K. 85*. **Xizang**: Mt. Kenichunpo, eastern and western Salwin and Irraway divide, *Rock J.F. 21991*; Tsarong, *Forrest G. 18964*; Shweli-Salwin divide, N of Ho-tou, *26738*. **Yunnan**: K'raikha-Salween divide, *Forrest G. 18371*; Salween-Mekong divide, *14402*; Shangpa Hsien, *Tsai H.T. 56560*; Shunning Hila, Wumulung, *Yu T.T. 16727*; Tengyueh valley 25°N, *Forrest G. 8678*; Wen shan Hsien, *Tsai H.T. 51702*; Salwin-Kui chiang divide, 28°24′N, 98°24′E, *Forrest G. 20844*; Chen-Kang Hsien, *Wang C.W. 72322*.

*Ecology.* In mixed forests, usually growing on yellow loam. Altitude: 600–2,000 m. Flowering May–June; fruiting August–September.

*Uses.* Wood used for furniture, tree grown as an ornamental because of its beautiful flowers.

*Collector's notes.* Bark gray, smooth; flowers greenish shaded purplish outside, white, ivory white, yellow-white to deep purple inside, fleshy, fragrant; leaves green above, pale green below, bruised leaves spicy-fragrant; fruit follicles conelike, green when young, orange-green, reddish yellow, red later.

*Note. Manglietia insignis* is a very widespread species. It therefore displays many variations in shape and size of the leaves as well as size and color of the flowers throughout the area of distribution.

11. **Manglietia lucida** B. L. Chen & S. C. Yang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 3: 94. 1988. TYPE: *B. L. Chen & C. N. Mai 87 T 002* (holotype, SYS). Figure 6.

Tree to 18 m high and 65 cm diam.; young twigs stout, 8–10 mm diam., grayish, smooth, often longitudinally wrinkled when dry, glabrous to minutely hairy. Stipules ferrugineous-pubescent, adnate to the base of the petiole, 3–4(–11.5) cm long. Leaves coriaceous, glabrous on both sides, with slightly recurved margins, obovate, approximately three times as long as broad, dark green and glossy above, often pale green below, 27–44 × 11–16 cm; apex acuminate, acumen 10–25 mm long; base cuneate, decurrent with two ridges into the petiole; midrib lengthwise sulcate above, rather elevated below; nerves in 13–19 pairs, curved upward and meeting in an intramarginal vein; all lesser veins forming a coarse reticulation on rather dull upper faces; petiole glabrous, often conspicuously thickened toward its base, 3.6–6 cm long, stipular scars 16–45 mm long. Peduncle pubescent as stipules, ca. 1.4 cm long and 6 mm thick, pedicle with same indumentum, 5–6 mm long; spathaceous bract only one, rather thick coriaceous, broadly obovate, at the base of pedicle, its outside face pubescent, 83 × 69 mm. Tepals 9(–11), purple, the outer 3 narrowly obovate, fleshy, 12–14 × 5.8–6 cm, the inner 6–8 in two rows, shorter and narrower than the outer tepals. Stamens numerous. Gynoecium ovoid, ca. 2.7 × 1.8 cm, carpels 70–80, glabrous, nearly entirely connate when young. Fruits ovoid-globose, 9.5 × 8–10 cm, torus with scars of perianth and stamens ca. 3 × 2 cm; fruiting peduncle ca. 4.5 × 1 cm, pedicle ca. 2.5 × 1 cm, ripe carpels ligneous, 20–35 × 8–10 mm, abaxial part 10–15 mm long, dehiscing along the dorsal suture at first and later also along the ventral suture. Seeds ca. 3 in each carpel.

*Distribution.* CHINA: **Southeastern Yunnan**: Maguan, *B. L. Chen & C. N. Mai 87 T 002*.

*Ecology.* In secondary forest. Altitude: 550–670 m. Flowering March–May; fruiting September–October.

*Note. Manglietia lucida* is apparently most closely allied to *Manglietia garrettii* and *Manglietia grandis*. It differs from the former by the obovate leaves, glabrous leaves and petioles, and bigger flowers, and from the latter by the pubescent stipules and peduncles, as well as by its smaller fruits.

12. **Manglietia megaphylla** Hu & Cheng, Acta Phytotax. Sin. 1: 159. 1951. TYPE: China. Yunnan: Faadou, Sichour Hsien, 1,100 m, *C. W. Wang 85156* (holotype, PE not seen). Figure 7.

Tree to 25 m high and 85 cm diam.; buds, young twigs, stipules, petiole, midrib and nerves below, and peduncles densely villous with rather long, undulate to curly, dark brown or rufous hairs; twigs stout, 8–12 mm diam., black-brown. Stipules adnate to the base of the petiole. Leaves thinly coriaceous, dark green, glabrous above, pale green, scattered-villous with long, undulate to curly, dark brown hairs below, obovate, 23–40 × 9.4–17 cm; apex acute to abruptly short-acuminate, base cuneate; nerves visible beneath, in 20–22 pairs; reticulation coarsely netted, prominent on both sur-

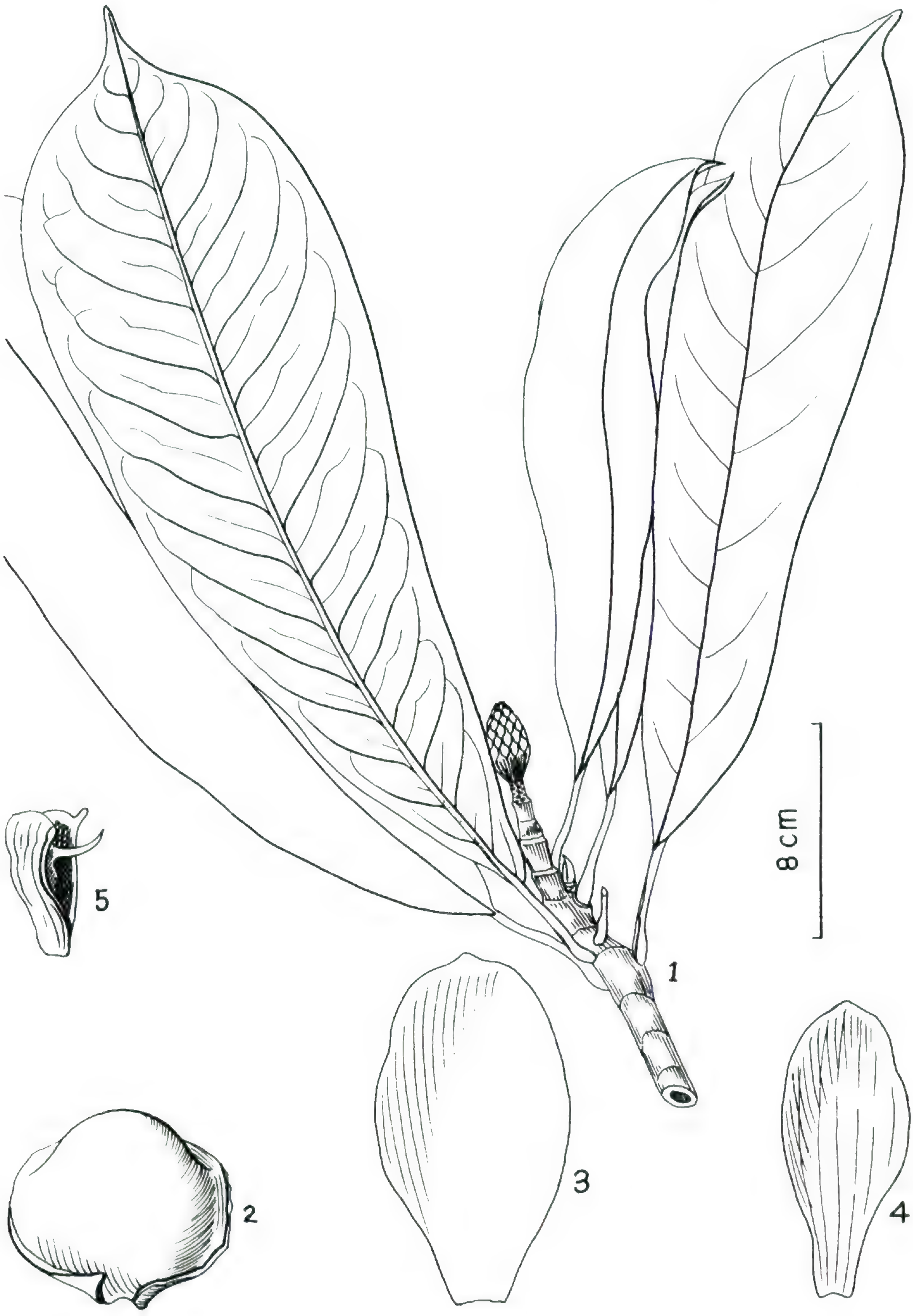


FIGURE 6. *Manglietia lucida* B. L. Chen & S. C. Yang.—1. Fruiting branch.—2. Bract.—3. Outer tepal.—4. Inner tepal.—5. Follicle. Based on *SYS 161496 = Chen Bao Liang 87 T 002*. Drawing by Xie Qing Jian.

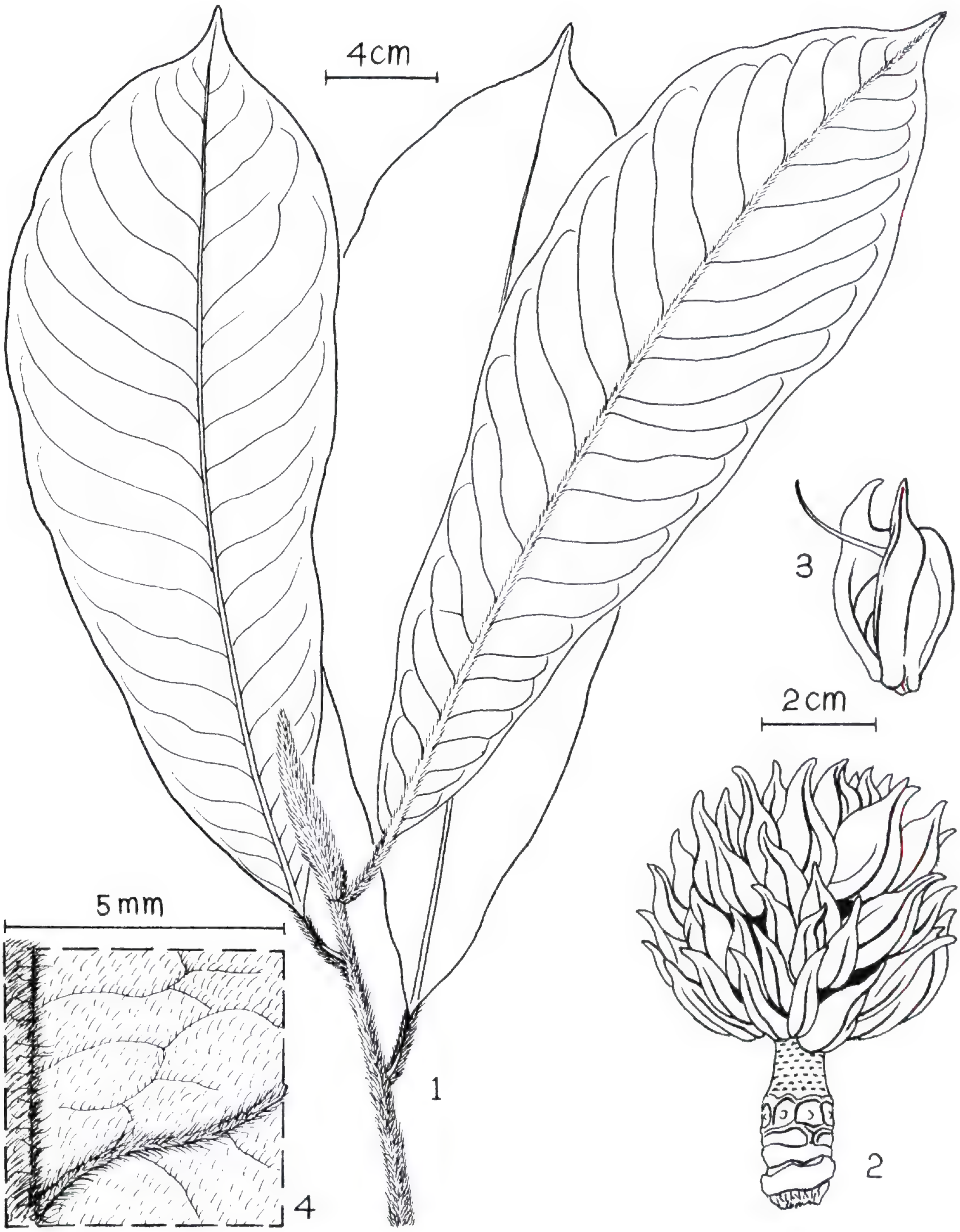


FIGURE 7. *Manglietia megaphylla* Hu & Cheng.—1. Branch with flower bud.—2. Fruit.—3. Follicle.—4. Undersurface of leaf. Based on *SYS 161435* = *Chen Bao Liang 87 T 102*. Drawing by Xie Qing Jian.

faces. Petiole usually dilatate toward the base, 1.5–3.7 cm long, stipular scars 0.7–3 cm long. Flowers not seen. Fruits ovoid to globose or oblong, ca. 7–9 × 6.5–8.5 cm; carpels 57–65, 2.5–3 cm long, apex with sharp beak 4–7 mm long, slightly recurved, dehiscing along the dorsal and the ventral suture; fruiting peduncles stout, ca. 1–3 × 1–1.3 cm. Pedicle 6 mm.

*Distribution.* CHINA. **Guangxi**: Donglin, *Chang C.C. 11438.* **Yunnan**: Maguang, *Chen B.L. GS 9 5*; Si-chour-hsien, Faa Doou, *Feng K.M. 11808.*

*Ecology.* In evergreen broad-leaved forests. Altitude: 800–1,500 m. Flowering April; fruiting September–October.

*Uses.* Wood straight-grained, coarse-textured and durable, moderately light and soft, commonly used for construction work, furniture, and plywood.

*Collector's note.* Fruit pale green, globose.

*Note.* In *Manglietia megaphylla* the distinguishing characters are the rufous indumentum with dense and long hairs, large leaves, and ovoid to oblong-ovoid fruits.

13. **Manglietia microtricha** Law, Bull. Bot. Res. (China) 5(3): 125, t. 4. 1985. TYPE: *Tibet Complex Exped. 74-1847* (holotype, PE not seen).

Tree to 30–40 m high, 40–60 cm diam.; young twigs stout, 6–10 mm diam. Stipules appressed brown pubescent, adnate to the base of the petiole, scars 6–13 mm long. Leaves coriaceous, green, glabrous above, glaucous beneath, obovate, 13–16 × 5–7 cm; apex short-acuminate, base cuneate; nerves in 15–17 pairs, reticulation fine, densely netted, prominent on both sides when dried. Petiole 2–2.5 cm long. Flower not seen. Fruiting peduncle ca. 1.5 cm long. Fruit ovoid, ca. 6 cm long, the dorsal face of the ripe carpel narrowly ellipsoid, appressed brown pubescent, with a ca. 3-mm-long beak at the apex. Seeds brownish, 1.5–2 cm long.

*Distribution.* CHINA. **Xizang** (Moyuo).

*Ecology.* In evergreen broad-leaved forest. Altitiude: 2,000 m. Fruiting September–October.

*Note.* No collections of this species were available; thus, based on Law's original description, *Manglietia microtricha* seems closely related to *Manglietia szechuanica.*

14. **Manglietia moto** Dandy, Notes Roy. Bot. Gard. Edinburgh 16: 128. 1928. TYPE: *K. P. To, W. T. Tsang & U.K. Tsang 180 in C. C. C. 12179* (holotype, A; isotypes, MO, SYS, UC).

Tree to 20 m high, 60 cm diam.; buds, young twigs, stipules, petiole, midrib below, bracts and peduncles densely villous with rather long crispy to curly dark brown to rufous hairs; young twigs 4–5 mm diam. Leaves green, glossy above, scattered-hairy with long, undulate to curly dark brown hairs beneath, glabrescent later, coriaceous, (narrowly) obovate, 11–19 × 5–7 cm; apex mucronate to acuminate, base cuneate to broadly cuneate, nerves in 9–19 pairs, reticulation obscure on both sides; petiole lengthwise narrowly sulcate above, 1.5–3.7 cm long, stipular scars narrowly triangular, 0.4–1.5(–3) cm long. Peduncles 4.3–9 cm × 4–6 mm, pedicle absent. Flowers fragrant; tepals 9, creamy white, the outer 3 coriaceous, oblong to ovate-oblong, ± hairy outside at the base, 3.7–5.7 × 2–2.5 cm, the inner 6 thick and fleshy, spathulate to obovate, slightly concave, the innermost ones usually becoming short-clawed toward the base, 9–12 × 1–1.8 cm; stamens numerous, 1.1–1.4 cm long, connective appendage semirounded or sometimes with a short, sharp tip, 1–1.5 mm long, filaments glabrous, ca. 1 mm long; gynoecium broadly ovoid, 1.3–1.5 × 1–1.2 cm, number of carpels 48–71; styles ca. 2 mm long; scars of the fallen perianth and stamens 9–12 × 4–7 mm. Fruiting peduncles ca. 11 × 0.5–0.6 cm. Fruits ovoid, 5–7 × 3.5–6 cm; carpels papilliferous on the dorsal face, apex with a ca. 2–3-mm-long beak. Seeds ovoid to elliptic, 6–9 × 4–6 mm, 6–9 in each carpel.

*Distribution.* CHINA. **Guangdong**: Wat Shui Shan, North river region, *Chun W.Y. 7353*; Yuyuen distr., *Ko S.P. 53514*; also reported form Ruyuan, Yaoshan, Yingteh, Lokchong, and Huanshuishan. Western, central, and northern Guangxi (He Xian, Cangwu Xi). Southern Hunan.

*Ecology.* In mixed forests. Altitude: 400–900 m. Flowering May–June; fruiting August–September.

*Uses.* Wood fine-textured, soft, used for general construction work and furniture.

*Collector's note.* Bark dull gray, flowers creamy white.

*Notes.* See Dandy (1928a). *Manglietia moto* is a notable species and is easily distinguished by its rufous indument and long peduncles.

*Manglietia rufibarbata*, which was originally collected from Vietnam, has not been recorded in China so far as we know. In our opinion, it closely resembles *Manglietia moto* in all characters, except for its stout peduncles and the fruits with rufous hairs. Because we have not seen sufficient material of *Manglietia rufibarbata*, we still maintain it here.

The type was identified as *Magnolia kwangtungensis* Merr. by Merrill (1927a) = *Manglietia fordiana* Oliver var. *kwangtungensis.*

15. **Manglietia pachyphylla** Chang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 53.

1961. TYPE: *P. S. Wang & H. H. Chiu 241* (holotype, SYS). Figure 8.

*Manglietia crassipes* Law, Bull. Bot. Res. (China) 2: 133. 1982. TYPE: China. Guangxi: Jinxiu Xian, 1,300 m, *Q. H. Lu 4319* (holotype, IBK not seen).

Tree 16 m high and 30 cm diam.; bark gray-black; twigs dull black, stout, ca. 1 cm diam., glabrous, covered with a waxy substance; stipules brown-villous, adnate to very base of the petiole. Leaves coriaceous, thick, rigid when dry, glabrous, dark glossy green above, pale green, minutely pubescent beneath, (narrowly) obovate or elliptic, 13–32 × 5–10 cm; apex blunt, short-acuminate; base cuneate; nerves in 8–14 pairs, faint on both surfaces, reticulation obscure. Petiole stout, sulcate above, 3–5 cm long, stipular scars 1–7 mm long. Peduncles minutely pubescent, ca. 1.7–2 × 0.7 cm, pedicle ca. 4 mm long; bract only one, broadly ovate, coriaceous, glabrous, ca. 4.8 × 7 cm. Flowers fragrant, tepals 9, white, the outer 3 oblong, coriaceous, 5.5–8 × 3.2–3.5 cm, the inner 6 obovate or broadly obovate, attenuate toward the base, convex, thick and fleshy, 3.2–4.3 × 2.5–3 cm, the innermost tepals usually short-clawed basally; stamens 0.7–1.2 cm long, connective appendage with rounded apex, ca. 1 mm long, filaments glabrous, ca. 1 mm long; gynoecium ovoid, ca. 2.2 × 1.8 cm; styles glabrous, ca. 1 mm long; the torus with scars of perianth and stamens ca. 1.5 × 0.7 cm. Fruiting peduncles 3–5.5 × 1–1.2 cm. Fruits ellipsoid, 5–7 × 4.5 cm; ripe carpels 38–46, ca. 1.5–2.5 mm long, short-beaked. Seeds 3–4 in each carpels, flat globose, 5–6 mm diam.

*Distribution.* CHINA. **Guangdong**: Conghus Xian, *Guang 242*; Tsung-hwa District, Sam Kok Shan, *Wang P.S. & Chiu, H.S. 241, Tsang W.T. 25175*. **Guizhou**: Anlong Xian, *Huangshan Exped. 3049*. Also reported from Guangxi (Dayaoshan and Jinxiu Shan).

*Ecology.* In evergreen broad-leaved forests. Altitude: 800–1,500 m. Flowering May; fruiting August–September.

*Uses.* The timber is used for general construction work, furniture and plywood; the tree is grown also as an ornamental plant because of its handsome crown.

*Notes.* The type specimen of *Manglietia crassipes* has not been seen. However, according to the published description and the collections examined, it is clear that *Manglietia crassipes* is conspecific with *Manglietia pachyphylla*.

16. **Manglietia szechuanica** Hu, Bull. Fan. Mem. Inst. Biol. (Peiping) 10: 117. 1940. TYPE: *T. T. Yu 3105* (holotype, PE; isotype, A).

Tree 15 m high and 30 cm diam.; young twigs green, 4–5 mm diam., at first yellowish villous, soon glabrescent or only hairy at the nodes; stipules pubescent, adnate to the base of the petiole. Leaves glabrous above, pale green, appressed-pubescent with short, straight, brown hairs on the surface and with rather long, straight, colorless to yellowish hairs along midrib and margins beneath, coriaceous, narrowly obovate, 13–20 × 4–7.3 cm; apex mucronate to acuminate, acumen 15–17 mm long; base narrowly cuneate to cuneate; midrib impressed above, elevated below, white villous with brown pigment, nerves fine in 8–19 pairs, reticulation coarse. Petiole white villous or later glabrescent, 1.5–2.5 cm long, stipular scars 9–11 mm long. Peduncles villous, glabrescent, 1–1.6 × 0.4–0.5 cm, pedicles 3–4 mm long. Flowers white; tepals 9, the outer 3 ovate-oblong, greenish with a flush of purple, sparsely villous, 4–5.5 × 2–2.8 cm, the inner 6 oblong to obovate, short-clawed at base, 4.5–6 × 1.5–3 cm; stamens 1.2–2 cm long, connective appendage triangular; gynoecium ovoid-ellipsoid, 1.7–2.5 × 1.5–3 cm, carpels 42–58, the lower narrowly ellipsoid, yellowish pubescent, 8–10 mm long. Styles glabrous, 4–6 mm long. Scars of perianth and stamens 7–10 × 5 mm.

*Distribution.* CHINA. **Northern Yunnan**: Suijiang, *Sun B., S. 341*. **Southern and central Sichuan**: Omei Xian, *Chow H.C. 11944*; Pingshan, *Yu T.T. 3105*.

*Ecology.* Altitude: 1,400–1,800 m.

*Collector's note.* Flowers pink or purple-red, scented. Bark grayish brown, smooth; leaves dark green above, yellowish brown with long hairs beneath.

17. **Manglietia ventii** Tiêp, Feddes Repert. 91, 9–10: 560. 1980. TYPE: China. Yunnan: Dinbian Hsien, alt. 880 m, 9 Aug. 1953, *P. I. Mao 2842* (LE not seen).

Tree to 30 m high. Young twigs 2–3.5 mm diam., black-gray, densely appressed-tomentellous with short, straight, glistening, yellowish hairs, old ones ± gray-pubescent to glabrescent. Stipules yellowish appressed-tomentellous, adnate to the base of the petiole, scars 1–2 cm long. Leaves usually crowded at the end of the twigs, chartaceous to thinly coriaceous, elliptic, broadly elliptic, obovate-elliptic to obovate, sometimes unequal; glabrous above, appressed-tomentose with short, straight, glistening, yellowish to silver hairs beneath, 9–18

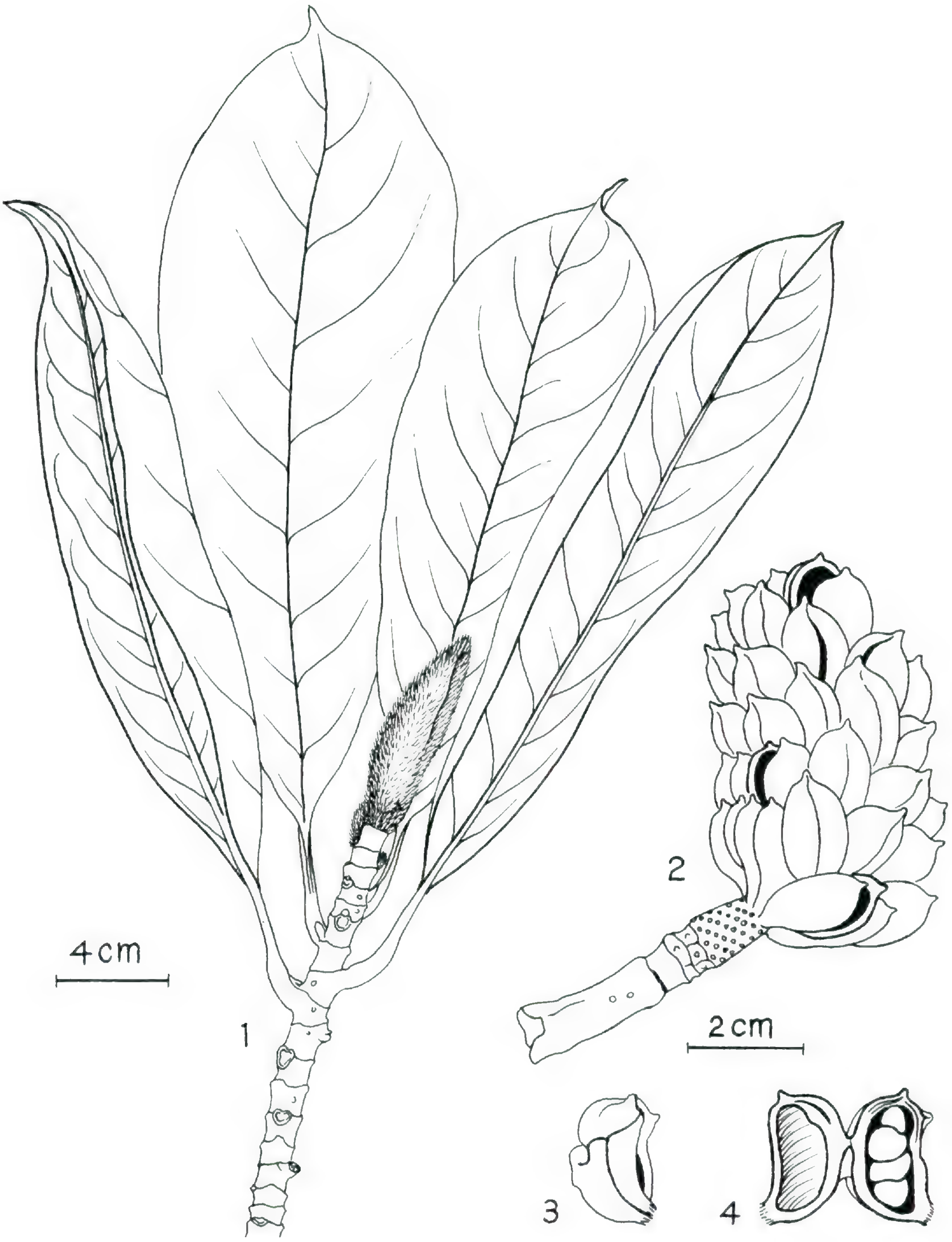


FIGURE 8. *Manglietia pachyphylla* Chang.—1. Branch with flower bud.—2. Fruit.—3. Follicle.—4. Open follicle with seeds. Based on *SYS 121334, Anonymous 241.* Drawing by Xie Qing Jian.

× 2.2–6.5 cm; apex short-acuminate to acuminate, acumen 3–17 mm long, base cuneate to obtuse; midrib impressed above, elevated below, densely pubescent to glabrescent, nerves fine, in 12–16 pairs, obscure above, visible beneath, reticulation lax, faint on both sides. Petiole slender, tomentellous, with same hairs as the young twigs, glabrescent, 2.6  3 cm long. Flower not seen. Fruit-

ing peduncle yellowish appressed-tomentose, 1–1.5 × 0.4–0.6 cm, with a bract scar, pedicle absent. Fruit ovoid to long-globose, 3.5–7 × 2.5–4.5 cm; ripe carpels ca. 64, long-ovoid, the lowest carpels decurrent along the torus, ± yellowish pubescent, especially toward the base of the lowest carpels, beak rather long, erect or recurved, dehiscing along the dorsal suture, 2–2.2 cm long; torus with 6–9 × 7 mm scars of perianth and stamens; scars of the fallen tepals ca. 10. Seeds subcordate to ovoid, ± impressed, 1–3 in each carpel, 7–7.5 × 5–6 mm.

*Distribution.* China and Vietnam. In CHINA. **Southeastern Yunnan**: Ping-pien Hsien, *Tsai H.T. 61619.*

*Ecology.* Altitude: 880 m.

**II-2. Manglietia** section **Manglietiastrum** (Law) Nooteboom, *Manglietiastrum* Law, Acta Phytotax. Sin. 11: 72, t. 2. 1979. *Magnolia* sect. *Manglietiastrum* (Law) Noot., Blumea 31: 91. 1985. TYPE SPECIES: *Manglietiastrum sinicum* Law.

Stipules free from petiole. Young leaves spreading in bud. Gynophore present.

18. **Manglietia sinica** (Law) B. L. Chen & Nooteboom, comb. nov. *Manglietiastrum sinicum* Law, Acta Phytotax. Sin. 17: 73, t. 2, 3. 1979. *Magnolia sinica* (Law Yuh-wu) Noot., Blumea 31, 1: 91, photo. 3. 1985. TYPE: China. Yunnan: Xichou, 1,550 m, *Law & Wang 6-75* (IBSC, v. spont.).

Tree to 40 m high and 1.2 m diam.; bark gray, longitudinally fine-fissured; trunk somewhat buttressed at the base; plant entirely glabrous; twigs dark green when young, faint brown when old; stipules free from the petiole. Leaves coriaceous, dark shining green above, pale green beneath, narrowly obovate, 15–26(–30) × 5–8(–9.5) cm; apex short-acuminate, with ca. 5-mm-long acute tip, base cuneate; margin slightly revolute; nerves in 13–16 pairs, reticulation coarse, prominent on both surfaces when dry. Petiole smooth above, slightly thickened at base, 1.5–2 cm long. Tepals 9, 3-merous, in 3 whorls; stamens ca. 65, connective appendage long-pointed; carpels 13–16. Fruits green at first, slightly flushed, obscure brown when dry, ovate, oblong-ovoid to obovoid, 5–8.5 × 3.5–6.5 cm; carpels thick woody, narrowly oblong-elliptic to obovoid-elliptic, 2.5–4 × 1.5–2.5 cm, opening along the ventral suture and splitting at the apex, dorsal faces conspicuously lenticellate; gynophore ca. 1 × 1.3 cm. Seeds 1–3 in each carpel, elliptic, compressed laterally, 1–1.3 cm wide, ca. 7 mm thick.

*Distribution.* CHINA. **Southeastern Yunnan**: Xichou, *Chen B.L. 87 F 180.*

*Ecology.* In evergreen broad-leaved rainforest. Altitude: 1,300–1,500 m. Flowering April; fruiting September–October.

*Note.* *Manglietia sinica*, a magnificent tree, is confined to a small area in southeastern Yunnan. One of the authors has investigated it several times in the field. The species possesses the chief diagnostic characters of *Manglietia*, e.g., habit of tree, the terminal flowers with 9 tepals, and more than 2 ovules in each carpel. Therefore, we prefer to include it in *Manglietia*. On the other hanad, there occur some remarkable characters in this species, such as the petioles without stipular scars and the gynoecium with a short gynophore. These features easily distinguish it from the other species in this genus and warrant its status as a section. The sections in *Magnolia* are based on the same kind of characters.

**III. Kmeria** (Pierre) Dandy, Kew Bull. 1927: 262. 1927. *Magnolia* subg. *Kmeria* Pierre, Fl. Forest. Cochinch. 1: sub t. 1. 1880. TYPE SPECIES: *Kmeria duperreana* (Pierre) Dandy.

*Tree.* Stipules adnate to the petiole. Flowers terminal, solitary, unisexual; tepals 6–7, 3-merous, subequal; anthers dehiscing introrsely, the connective produced into a short or moderately elongated appendage. Gynoecium sessile. Carpels comparatively few, concrescent. Ovules 2. Fruiting carpels woody, separating on dehiscence, dehiscing completely along the ventral suture and partly along the dorsal suture, thus finally becoming bifid. Seeds 1–2 in each carpel.

*Distribution.* Two species, southern China to Indochina.

*Note.* This genus is closely related to *Magnolia*. It could also be treated as a section close to section *Gwillimia*. In China the only species that occurs is *Kmeria septentrionalis*.

1. **Kmeria septentrionalis** Dandy, J. Bot. 69: 233. 1931. TYPE: *R. C. Ching 5247* (holotype, BM; isotypes, NY, PE).

Tree to 18 m high; bark gray; twigs green, ± glaucescent when dry, appressed short pubescent. Stipules glabrous or sparsely pubescent, adnate to rather high on the petiole, stipular scars nearly to

its apex. Leaves coriaceous, bright green, glabrous above, greenish, glabrous or sparsely pubescent toward the base when young beneath, elliptic-oblong or obovate-oblong, 8–15 × 3.5–6 cm; apex retuse, base broadly cuneate; midrib prominent below, nerves visible on both sides, in 12–17 pairs, reticulation prominent on both surfaces when dry. Petiole slender, pubescent to glabrescent, 2–3.5 cm long. Brachyblast glabrous, 1.5 cm long. Flower bud (the male flower) subglobose; tepals 6; stamens 1–1.5 cm long, connective appendage triangular, 1–2.5 mm long.

*Distribution.* CHINA. **Northern and central Guangxi**: Huanjiang, *Pang C.F. 28*; southeastern Luchen, *Ching R.C. 5247*. **Yunnan**: Huang Jingin, Mar Li Po, *Wang C.W. & Liu 83157*; Maguan, *Chen B.L. 87 F 173*.

*Ecology.* In evergreen forest. Altitude: 300–500 m. Flowering May–June.

*Collector's notes.* Tree with a large dense crown; bark gray; leaves evergreen; flowers white, fragrant.

*Note.* This species is closely related to *K. duperreana* (Pierre) Dandy. Recently, a new record of *K. duperreana* in Libo of Guizhou was reported, but we have not seen a collection from that locality.

TRIBE MICHELIEAE

**IV. Michelia** L., Sp. Pl.: 536. 1753. *Champaca* Adans., Fam. Pl. 2: 365, 537. 1763. *Sampacca* O. Kuntze, Rev. Gen. Pl. 1: 6. 1891. TYPE SPECIES: *Michelia champaca* L.

*Liriopsis* Spach, Hist. Natur. Veget., Phanerog. 7: 460. 1839, non *Liriopsis* Reichenb. (1828). TYPE SPECIES: *Liriopsis fuscata* (Andr.) Spach.

*Paramichelia* H. H. Hu, Sunyatsenia 4: 142. 1940. TYPE SPECIES: *Paramichelia baillonii* (Pierre) Hu.

*Tsoongiodendron* W. Y. Chun, Acta Phytotax. Sin. 8: 7. 1963. TYPE SPECIES: *Tsoongiodendron odorum* Chun.

Trees or shrubs. Stipules adnate to or free from the petiole. Flowers bisexual, on short brachyblasts in the axils of the leaves, growth monopodial. Tepals 6–21, 3–6-merous, subequal or rarely the outer whorl different. Anthers latrorse or sublatrorse (to introrse), connective produced into a short or elongated appendage. Gynoecium stipitate; carpels many to few (rarely 1), free or connate; ovules 2 to many; follicles free, ± spaced along the torus, dehiscing along the dorsal suture, finally becoming 2-valved, or concrescent, forming a fleshy syncarp, tardily and irregularly dehiscent, or a woody syncarp, the upper parts of the carpels falling away while also dehiscing along the dorsal suture, the basal parts remaining attached to the torus with their suspended seeds.

*Distribution.* About 40 species, in Southeast Asia from India and Sri Lanka eastward to southwestern and southeastern China, northeastward to southern Japan and southeastward into Indonesia (not in Sulawesi and New Guinea).

KEY TO THE SECTIONS OF *MICHELIA*

1. Tepals very dissimilar, those of the outer whorl much shorter and narrower those of the inner whorls; fruit apocarpous; stipules free from petiole. ..... **IV-2.** *Michelia* sect. *Anisochlamys*
1. Tepals of the outer whorl sometimes smaller and thinner than those of the inner whorls, but not very dissimilar; fruits apocarpous or syncarpous; stipules free from or adnate to petiole. ..... 2
2(1). Fruits syncarpous; stipules adnate to petiole. 3
2. Fruits apocarpous; stipules free from or adnate to petiole. ..... 4
3(2). Tepals 9; fruits 13–16 cm. ..... **IV-5.** *Michelia* sect. *Tsoongiodendron*
3. Tepals 12; fruits 3–9 cm. ..... **IV-6.** *Michelia* sect. *Paramichelia*
4(2). Tepals 6, or occasionally 4, 2-merous; stipules free from petiole. ..... **IV-3.** *Michelia* sect. *Dichlamys*
4. Tepals 6–21, 3–6-merous; stipules free from or adnate to petiole. ..... 5
5(4). Petioles not exceeding 10 mm, stipules adnate to it; shrubs or small trees. ..... **IV-4.** *Michelia* sect. *Micheliopsis*
5. Petioles longer than 10 mm, stipules free or adnate. ..... **IV-1.** *Michelia* sect. *Michelia*

KEY TO THE SPECIES OF *MICHELIA*
(primarily based on floral characters)

1. Tepals 6 or 7. ..... 2
1. Tepals 8–20. ..... 10
2(1). Petiole 2–10 mm. ..... 3
2. Petiole 10–45 mm. ..... 6
3(2). Gynoecium longer than androecium. ..... 4
3. Gynoecium shorter than androecium, often entirely hidden. ..... 5
4(3). Petiole 5–10 mm long, stipular scars nearly to its apex; tepals 22–35 mm long; gynophore 5–8 mm long; gynoecium ovoid to oblong. ..... 33. *Michelia yunnanensis*
4. Petiole 3–5 mm long, stipular scars to halfway; tepals 15–25 mm long; gynophore 1–3 mm long; gynoecium cylindric. ..... 32a. *Michelia figo* var. *figo*
5(3). Stipules adnate to petiole; petiole 2–4 mm; flower purple or red; stamens 10 mm long; gynoecium cylindric. ..... 32b. *Michelia figo* var. *crassipes*
5. Stipules free; petiole 10 mm; flower white; stamens 11–15 mm long; gynoecium ellipsoid. ..... 26. *Michelia angustioblonga*
6(2). Leaves glabrous. ..... 7

6. Leaves hairy beneath at least when young. 8
7(6). Base of leaf broadly cuneate or attenuate-cuneate, nerves in 7–17 pairs; brachyblast pubescent, 7–15 × 3–9 mm; gynophore and carpels glabrous; twigs and stipules pubescent; scars of perianth and stamens along torus under fruit 6–8 mm long. ..... 30. *Michelia martinii*
7. Base of leaf cuneate or rounded, nerves in 9–12 pairs; brachyblast tomentellous or puberulous, 3–11 × 2–4 mm; gynophore and carpels silver gray tomentellous; twigs tomentellous; stipules glabrous, puberulous, or tomentellous; scars of perianth and stamens along torus under fruit 4–5 mm long. ..... 28. *Michelia chapensis*
8(6). Leaves 1.5–2.5 cm broad; shrub to 4 m high; leaf apex obtuse; outer tepals spathulate, 18–20 × 4–5 mm; gynoecium hidden by the stamens; gynophore 3–4 mm long. ..... 26. *Michelia angustioblonga*
8. Leaves 2.8–16.5 cm broad; tree to 15–18 m high; leaf apex short-acuminate, acuminate, or acute; outer tepals obovate, oblong, or elliptic; gynoecium ovoid or cylindric; gynophore 5–10 mm long. ..... 9
9(8). Pedicle present; twigs appressed tomentellous; stipules glabrous or tomentellous; leaves 2.8–4.5 cm broad, reticulation rather obscure; petiole not dilated at base; gynoecium cylindric. ..... 29. *Michelia leveilleana*
9. Pedicle absent; twigs pubescent; stipules pubescent; leaves 4.5–10(–16.5) cm broad, reticulation distinct; petiole dilated at base; gynoecium ovoid. ..... 27. *Michelia balansae*
10(1). Stipules free. ..... 11
10. Stipules adnate to petiole. ..... 25
11(10). Leaves glabrous. ..... 12
11. Leaves hairy beneath at least when young. 17
12(11). Brachyblast 10–40 mm long; outer tepals 5–8 cm long; stamens 13–25 mm long. ..... 13
12. Brachyblast 2.5–6 mm long; outer tepals 1–3 cm long; stamens 2.5–10 mm long. 15
13(12). Leaves glaucous beneath, nerves in 12–14 pairs; stipules silky; petiole hairy; outer tepals 35 mm broad; gynoecium golden puberulous, ca. 20 mm long. ..... 13. *Michelia ingrata*
13. Leaves not glaucous beneath; stipules glabrous or pubescent; petiole glabrous; outer tepals 15–40 mm broad; gynoecium glabrous. ..... 14
14(13). Plant entirely glabrous; reticulation of leaf densely netted, nerves in 7–12 pairs; inner tepals 4.5–5 cm long; gynoecium 10–13 mm high; scars of perianth and stamens along torus under fruit 5–6 mm long. ..... 18. *Michelia maudiae*
14. Plant hairy at least in innovations; stipules pubescent; reticulation laxly netted, nerves in 9–20 pairs; inner tepals 5.5–7 cm long; gynoecium 17–20 mm high; scars of perianth and stamens along torus under fruit 20–22 mm long. ..... 15. *Michelia lacei*
15(12). Twigs glabrous, 1–2 mm diam.; stipules puberulous; midrib of leaf prominent above, at least toward base; tepals very dissimilar, outer tepals small, nearly linear, ca. 1 mm broad; gynophore under fruit 2–3 mm long. ..... 25. *Michelia hypolampra*
15. Twigs hairy at least when young; stipules pubescent or tomentellous; midrib of leaf not prominent above; tepals subsimilar, outer tepals obovate or spathulate; gynophore under fruit 10–17 mm long. ..... 16
16(15). Gynoecium glabrous, cylindric, 10–12 mm long; stipules tomentellous; reticulation distinct; petiole dilated at base; filaments 2.5–3 mm long. ..... 5. *Michelia coriacea*
16. Gynoecium hairy, ovoid, 4–6 mm long; stipules pubescent; reticulation of leaf rather obscure; petiole not dilated at base; filaments 1 mm long. ..... 4. *Michelia compressa*
17(11). Outer tepals 1–3 cm long. ..... 18
17. Outer tepals 3.1–9 cm long. ..... 20
18(17). Pedicle present; leaves 5–10(–16.5) × 3–4(–7) cm, reticulation distinct; brachyblast silver or brown tomentellous, 6–10 mm long; connective appendage linguiform, 2–4 mm long; filaments 1.5–2 mm long; gynophore under fruit 5–8 mm long. ..... 19. *Michelia mediocris*
18. Pedicle absent; leaves 4–26 × 1.5–12.5 cm, reticulation rather obscure; brachyblast 3–6 or 13–25 mm long; connective appendage triangular, 0.5–1 mm long; filaments 1–6 mm long; gynophore under fruit 10–30 mm long. ..... 19
19(18). Gynophore 12–15 mm long; twigs tomentose; stipules silky; brachyblast 13–25 mm long; outer tepals 16–24 mm broad; stamens 17–20 mm long, filaments 4–6 mm long; gynoecium cylindric, 17–20 mm high; number of ovules per carpel 10; follicles hairy. ..... 10. *Michelia foveolata*
19. Gynophore 2–6 mm long; twigs puberulous; stipules pubescent; brachyblast 3–6 mm long; outer tepals 3–10 mm broad; stamens 2.5–7 mm long, filaments 1 mm long; gynoecium ovoid, 4–6 mm high; number of ovules per carpel 2–8; follicles glabrous. ..... 4. *Michelia compressa*
20(17). Leaves glaucous beneath; twigs villous, 5–7 mm diam.; stamens 17–22 mm long, filaments 4–6 mmm; gynoecium golden puberulent. ..... 13. *Michelia ingrata*
20. Leaves not glaucous beneath; twigs pubescent, tomentose, or tomentellous. ..... 21
21(20). Gynophore 10–15 mm long; stipules silky. 22
21. Gynophore 2–5 mm long; stipules pubescent or tomentellous. ..... 23
22(21). Filaments 3 mm long; twigs glabrous or pubescent; leaves minutely scattered hairy beneath, reticulation distinct, laxly netted; gynoecium 3–6 mm high; fruiting brachyblasts 5–7 cm long; follicles glabrous. ..... 17. *Michelia masticata*
22. Filaments 4–6 mm long; twigs tomentose; young leaves tomentose beneath, reticulation rather obscure, densely netted; gynoecium 17–20 mm high; fruiting brachyblasts 1.5–3 cm long; follicles hairy. ..... 10. *Michelia foveolata*
23(21). Leaves 6.5–14 × 4–6.5 cm; connective

appendage linguiform; twigs and stipules tomentellous; tepals 9–12, outer tepals 35–45 × 10–15 mm; gynoecium cylindric. ... 16. *Michelia macclurei*

23. Leaves (10–)12–20(–24) × 3.5–7 or 18–25 × 4–7.5 cm; connective appendage triangular; twigs pubescent or tomentose; stipules pubescent; tepals 9–12 or 13–17, outer tepals 32–36 × 10–12 or 45–70 × 20–25 mm; gynoecium ellipsoid. ... 24

24(23). Pairs of lateral nerves 11–15; twigs pubescent, 2–3 mm diam.; leaves finely appressed pubescent beneath, base cuneate or broadly cuneate; tepals 9–12, 45–70 × 20–25 mm; filaments 2–3 mm long; scars of perianth and stamens along torus under fruit 5–10 mm long. ... 2. *Michelia cavaleriei*

24. Pairs of lateral nerves 16–18; twigs tomentose, ca. 4 mm diam.; young leaves densely appressed tomentellous beneath, base rounded; tepals 13–17, the outer ones 32–45 × 10–12 mm; filaments 4 mm long; scars of perianth and stamens along torus under fruit 12–14 mm long. ... 1. *Michelia aenea*

25(10). Stamens 20–39 mm long. ... 26

25. Stamens 5–15 mm long. ... 27

26(25). Brachyblast 20–22 mm long; tree to 15 m high; twigs in innovations 8–12 mm thick; petiole dilated at base; stipular scars 7–10 mm long; brachyblast 10–12 mm thick; petiole absent; stamens 33–39 mm long, filaments 7–8 mm long; gynoecium shorter than androecium, often entirely hidden, 24 mm high; gynophore 6 mm long. ... 12. *Michelia fulva*

26. Brachyblast 30–35 mm long; treelet to 5–6 m high; twigs in innovations 2–3 mm thick; petiole not dilated at base; stipular scars 3–4 mm long; brachyblast 5–6 mm thick; petiole present; stamens 20–24 mm long, filaments 2–4 mm long; gynoecium longer than androecium, 15 mm high; gynophore 30 mm long. ... 7. *Michelia elliptilimba*

27(25). Outer tepals 10–30 mm broad. ... 28

27. Outer tepals 2.5–10 mm broad. ... 32

28(27). Pedicle present. ... 29

28. Pedicle absent. ... 30

29(28). Petiole hairy, 2.5–3 cm; stipular scars 15 mm long, leaf base cuneate, reticulation rather obscure; outer tepals 3; gynophore 4 mm long. ... 20. *Michelia microtricha*

29. Petiole 0.8–2.5 cm, glabrous; stipular scars 2–6 mm long; leaf base broadly cuneate or rounded; reticulation distinct; outer tepals 4 or 5, gynophore 5–12 mm long. ... 6. *Michelia doltsopa*

30(28). Connective appendage 2–4 mm long, narrowly triangular or linguiform; twigs sparsely minutely puberulous or tomentellous; leaves minutely appressed pubescent beneath, reticulation distinct; gynoecium 6–10 mm high; fruiting brachyblasts 5 mm thick. ... 14. *Michelia kisopa*

30. Connective appendage very short to long triangular, 0.5–3 mm; twigs pubescent or tomentose; young leaves densely or sparsely pubescent beneath, reticulation rather obscure; gynoecium 9–14 mm or 3–5 mm high; fruiting brachyblasts 2–4 mm thick. 31

31(30). Gynoecium ovoid to oblong, 3–5 mm high; petiole 3–5 mm long. ... 33. *Michelia yunnanensis*

31. Gynoecium cylindric, 9–14 mm high; petiole 9–25 mm long. ... 9. *Michelia floribunda*

32(27). Outer tepals 4–6. ... 33

32. Outer tepals 3. ... 34

33(32). Stipular scars 3–5 mm long; leaves elliptic or narrowly elliptic, reticulation rather obscure; brachyblast stout; gynoecium 9–15 mm high; gynophore 6–7 mm long. ... 22. *Michelia velutina*

33. Stipular scars 17–28 mm long; leaves ovate or narrowly ovate, reticulation distinct; brachyblast slender; gynoecium 7–12 mm high; gynophore 3–5 mm long. ... 3. *Michelia champaca*

34(32). Stipular scars 1–5 mm long. ... 35

34. Stipular scars 6–20 mm long. ... 36

35(34). Tepals 9–12; connective appendage ca. 0.5 mm long; stipules pubescent; fruiting brachyblasts 11 mm long and 8 mm thick; fruits 13.5–15.5 cm long; gynophore under fruit 20–25 mm long. ... 23. *Michelia wilsonii*

35. Tepals 12–15; connective appendage 1–3 mm; stipules tomentellous; fruiting brachyblasts 5–8 mm long and 3–4 mm thick; fruits 2.5–6 cm long; gynophore under fruit 10–15 mm long. ... 9. *Michelia floribunda*

36(34). Tepals 9, 15–20 × 5–7.5 mm; stamens 7.5–8.5 mm, connective appendage 0.5 mm; gynoecium ovoid, 3–4 mm, carpels 10–12; stipular scars 6–18 mm. ... 34. *Michelia odora*

36. Tepals 9–20, 19–50 × 6–23 mm; connective appendage 1–4 mm long; gynoecium ovoid or more often cylindric; carpels often more than 12; stipular scars 2–20 mm. ... 37

37(36). Stipular scars 14–20 mm; gynoecium 6–10 mm; tepals 9–15, 22–35 mm × 7–13 mm; connective appendage 2–4 mm. ... 14. *Michelia kisopa*

37. Stipular scars 2–4 mm; gynoecium 9–14 or 6–9 mm; tepals 12–20, 12–20 × 19–35 mm; connective appendage 1–3 mm. 38

38(37). Tepals 6–23 mm broad; gynoecium 9–14 mm; connective appendage 1–3 mm; stipular scars 2–14 mm. ... 9. *Michelia floribunda*

38. Tepals 2.5–7 mm broad; gynoecium 6–9 mm; connective appendage 1–2 mm; stipular scars 6–10 mm. ... 35. *Michelia baillonii*

## Key to the Species of *Michelia*
(primarily based on fruit characters)

1. Fruits with connate carpels, when mature the apical parts of the carpels falling, dehiscing along the dorsal suture or not, the basal parts remaining adnate to the torus, or apical parts falling in irregular masses. 2

1. Fruits consisting of free carpels, which dehisce along the dorsal suture, main nerve often persistent. ..... 3
2(1). Reticulation densely netted; fruits 3–9 cm long and 2.5–4.5 cm broad. ..... 35. *Michelia baillonii*
2. Reticulation laxly netted; fruits 13–16 cm long and 7–9 cm broad. .. 34. *Michelia odora*
3(1). Stipules adnate to the petiole. ..... 4
3. Stipules free. ..... 17
4(3). Stipular scars 11–28 mm long. ..... 5
4. Stipular scars 1–10 mm long. ..... 8
5(4). Pedicle present, at least 3 mm long; leaves elliptic or narrowly obovate, reticulation rather obscure; twigs tomentellous. ..... 20. *Michelia microtricha*
5. Pedicle absent or very short. ..... 6
6(5). Leaves minutely appressed pubescent, glabrescent beneath; twigs puberulous or tomentellous; fruiting brachyblasts 7 × 5 mm; follicles 8–14 × 7–10 mm. ..... 14. *Michelia kisopa*
6. Young leaves tomentose or pubescent beneath; twigs pubescent or tomentose; fruiting brachyblast 5–30 × 3–5 mm; follicles 7–20 × 7–14 mm. ..... 7
7(6). Leaves 1–5 cm broad; reticulation rather obscure; twigs tomentose; stipules tomentellous; fruiting brachyblast 5–8 mm long. ..... 9. *Michelia floribunda*
7. Leaves 3.4–12 cm broad; reticulation distinct; twigs and stipules pubescent; fruiting brachyblast 10–30 mm long. ..... 3. *Michelia champaca*
8(4). Petiole 2–5 mm (*Michelia yunnanensis* with very short petiole is also possible here). 9
8. Petiole 5.1–30 mm. ..... 10
9(8). Shrub to 2–5 m high; flower purple or red; fruiting brachyblast 10–20 × 3–5 mm. ..... 32b. *Michelia figo* var. *crassipes*
9. Shrub or treelet to 15 m high; flower white or yellow; fruiting brachyblast 7–25 × 2–4 mm. ..... 32a. *Michelia figo* var. *figo*
10(8). Pedicle present. ..... 11
10. Pedicle absent. ..... 13
11(10). Treelet to 5 or 6 m high; twigs silky, 2–3 mm diam.; stipules silky; leaves 16–22 × 7.5–10 cm, nerves in 9–14 pairs; petiole 2–2.5 cm; brachyblast 30–35 mm long; outer tepals 3; stamens 20–24 mm long; gynophore 30 mm long. ..... 7. *Michelia elliptilimba*
11. Tree to 15–30 m high; twigs pubescent or tomentellous; stipules pubescent or tomentellous; brachyblast 4–17 mm long; leaves 9–22 × 4–8 or 11–24 × 3.5–6.5(–8.5) cm, nerves 10–28 pairs; petiole 0.8–2.5 cm; outer tepals 4–6; stamens 8–15 mm long; gynophore 5–12 mm long. ..... 12
12(11). Scars of perianth and stamens along torus under fruit 5 mm long; twigs and stipules pubescent; reticulation of leaf rather obscure; petiole hairy. ..... 22. *Michelia velutina*
12. Scars of perianth and stamens along torus under fruit 7–10 mm long; twigs sparsely tomentellous; stipules tomentellous; reticulation distinct; petiole glabrous. ..... 6. *Michelia doltsopa*
13(10). Fruiting brachyblasts 2–4 mm thick. ..... 14
13. Fruiting brachyblasts 5–12 mm thick. ..... 15
14(13). Shrub or small tree 6–12 m; petiole 5–10 mm; stipular scar 3–7 mm; nerves in 7–9 pairs. ..... 33. *Michelia yunnanensis*
14. Tree to 28 m high; petiole 9–25 mm; stipular scar 2–14 mm; nerves in 8–14 pairs. ..... 9. *Michelia floribunda*
15(13). Young twigs 8–12 mm thick; stipules hispid; reticulation of leaf distinct; stipular scars 7–10 mm long; scars of perianth and stamens along torus under fruit 10 mm long. ..... 12. *Michelia fulva*
15. Young twigs 1–3 mm thick; stipules pubescent; reticulation rather obscure; stipular scars 1–5 mm long; scars of perianth and stamens along torus under fruit 2–5 mm long. ..... 16
16(15). Leaves glaucous beneath; twigs glabrous to tomentose; fruits 13.5–15.5 cm. ..... 23. *Michelia wilsonii*
16. Leaves not glaucous beneath; twigs pubescent; fruits 3.5–13 cm long. ..... 22. *Michelia velutina*
17(3). Leaves glabrous. ..... 18
17. Leaves hairy beneath at least when young. 25
18(17). Gynophore under fruit 2–3 mm long; midrib prominent above, at least toward base; fruits 3.5–4 cm long; follicles 2–4.5 × 1–2.5 cm with a stipe of 3–8 mm. ..... 25. *Michelia hypolampra*
18. Gynophore under fruit 8–30 mm long; midrib not prominent above. ..... 19
19(18). Leaves glaucous beneath; stipules silky; twigs 5–7 mm diam.; fruits 6–10 cm long; follicles sessile, 9–14 × 7–10 mm. ..... 13. *Michelia ingrata*
19. Leaves not glaucous beneath; stipules glabrous, pubescent, puberulous, or tomentellous. ..... 20
20(19). Scars of perianth and stamens along torus under fruit 20–22 mm long; fruits 7–10 cm long; twigs 4–6(–10) mm diam. ..... 15. *Michelia lacei*
20. Scars of perianth and stamens along torus under fruit 2–8 mm long. ..... 21
21(22). Plant entirely glabrous; twigs 2–3 mm diam.; leaves 9.5–17.5 × 3–7 cm; nerves in 7–12 pairs; petiole 1–3 cm; fruit 10–14 cm long; brachyblast 17–30 mm. ..... 18. *Michelia maudiae*
21. Plant hairy at least in innovations; brachyblast hairy. ..... 22
22(21). Reticulation rather obscure; twigs 1–2 mm diam.; leaves 4–12 × 1.5–3.5 cm; nerves in 8–15 pairs; fruits 5–7 cm long; brachyblast 3–8 mm long. .... 4. *Michelia compressa*
22. Reticulation distinct; twigs 2–7 mm diam.; leaves 5.5–18 × 2–6.5 cm; fruits 3–10 cm; brachyblast 6–25 mm. ..... 23
23(22). Twigs glabrous, sometimes pubescent, 2–4 mm diam.; stipules pubescent; fruits 6.5–

10 cm long; brachyblasts 13–14 × 4–9 mm. ..... 30. *Michelia martinii*
23. Twigs puberulous or tomentellous; stipules glabrous, puberulous, or tomentellous, leaf base cuneate or rounded. ..... 24
24(23). Reticulation of leaf laxly netted; twigs tomentellous; petiole not dilated at base; fruits 3–10 cm long; brachyblast 6–12 mm long; follicles 6–15 × 8–10 mm. ..... 28. *Michelia chapensis*
24. Reticulation of leaf densely netted; twigs puberulous; petiole dilated at base; fruit 3–6 cm long; brachyblast 8–25 mm long; follicles 18–25 × 12–17 mm. ..... 5. *Michelia coriacea*
25(17). leaves glaucous beneath. 13. *Michelia ingrata*
25. Leaves not glaucous beneath. ..... 26
26(25). Pedicle present. ..... 27
26. Pedicle absent. ..... 32
27(26). Leaves 1.5–2.5 cm broad, apex rounded. ..... 26. *Michelia angustioblonga*
27. Leaves 2.8–7.5 cm broad, apex acuminate or acute. ..... 28
28(27). Pairs of lateral nerves 16–18; twigs tomentose; scars of perianth and stamens along torus under fruit 12–14 mm long. ..... 1. *Michelia aenea*
28. Pairs of lateral nerves 9–15; twigs pubescent or tomentellous; scars of perianth and stamens along torus under fruit 3–10 mm long. ..... 29
29(28). Fruiting brachyblasts 3 cm long; twigs tomentellous; stipules glabrous or tomentellous; young leaves rufous pubescent beneath, apex acuminate or acute, reticulation rather obscure; pedicle 4–6 mm, tepals 6, gynoecium cylindric. 29. *Michelia leveilleana*
29. Fruiting brachyblasts 1–2.5 cm long. ..... 30
30(29). Twigs pubescent; stipules pubescent; leaves obovate or narrowly elliptic, 12–20 × 3.5–5.5 cm; petiole 1.5–3 cm; fruit 5–15 cm; gynophore 10–25 mm. 2. *Michelia cavaleriei*
30. Twigs tomentellous; stipules tomentellous; leaves elliptic or ovate, 5–14 × 3–6.5 cm; fruits 2–5 cm long; gynophore 5–10 mm. 31
31(30). Carpels 13–18; leaves 6.5–10 × 3–4 cm; petiole 1.5–2.5 cm. ... 19. *Michelia mediocris*
31. Carpels 28; leaves 6.5–14 × 4–6.5 cm; petiole 2.5–4 cm. ..... 16. *Michelia macclurei*
32(26). Leaves 1.5–2.5 cm broad. ..... 33
32. Leaves 2.6–16.5 cm broad. ..... 34
33(32). Apex of leaf rounded, reticulation distinct; treelet to 4 m high; leaves narrowly oblong, 6.5–10 × 1.5–2.5 cm; petiole 10–15 cm. ..... 26. *Michelia angustioblonga*
33. Leaves (narrowly) elliptic, 4–12 × 1.5–3.5 cm, apex acuminate or acute, reticulation rather obscure; petiole 5–22 mm. ... 4. *Michelia compressa*
34(32). Pairs of lateral nerves 16–19. ..... 35
34. Pairs of lateral nerves 8–15. ..... 37
35(34). Twigs pubescent, 2–5 mm diam.; leaves 8–28 × 4.5–10.5 cm, reticulation laxly netted; petiole 19–45 mm; nerves in 12–14 pairs; follicles 20–65 × 13–18 mm. ..... 27. *Michelia balansae*
35. Twigs tomentose; reticulation of leaf densely netted, nerves in 16–18 pairs; follicles 14–25 × 10–15 or 8–22 × 7–14 mm. 36
36(35). Scars of perianth and stamens along torus under fruit 5–7 mm long; stipules silky; reticulation of leaf rather obscure; follicles hairy. ..... 10. *Michelia foveolata*
36. Scars of perianth and stamens along torus under fruit 12–14 mm long; stipules pubescent; reticulation of leaf distinct; follicles glabrous. ..... 1. *Michelia aenea*
37(34). Twigs puberulous, 1–2 mm diam.; leaves 4–12 × 1.5–3.5 cm; fruits 5–7 cm. ..... 4. *Michelia compressa*
37. Twigs pubescent or tomentose. ..... 38
38(37). Twigs tomentose; leaf apex acuminate or acute, reticulation rather obscure; fruits 5.5–14 cm long; follicles 8–22 × 7–14 mm. ..... 10. *Michelia foveolata*
38. Twigs pubescent, leaf apex short-acuminate, reticulation distinct. ..... 39
39(38). Young leaves pubescent beneath, 8–28 × 4.5–16.5 cm; petiole dilated at base; fruits 4–12 cm long; follicles 2–6.5 × 1.3–1.8 cm. ..... 27. *Michelia balansae*
39. Leaves finely scattered appressed-pubescent beneath; petiole not dilated at base; fruits 5–53 cm long; follicles 6–14 or to 100. ..... 40
40(39). Reticulation of leaf laxly netted; stipules silky; fruit 10–53 cm long, follicles to 100. ..... 17. *Michelia masticata*
40. Reticulation of leaf densely netted; stipules pubescent; fruits 5–15 cm long, follicles 6–14. ..... 2. *Michelia cavaleriei*

**1. Michelia** section **Michelia.** *Michelia* L. *Champaca* Adans. *Sampacca* O. Kuntze.

*Liriopsis* Spach.

Stipules free from or adnate to the petiole. Bracts 2–6. Tepals 6–21, 3–6-merous, subsimilar or dissimilar with those of the outer whorl, smaller or thinner in texture than those of the inner whorl or whorls. Fruits apocarpous.

KEY TO THE SPECIES OF SECTION *MICHELIA*

1. Stipules adnate to petiole. ..... 2
1. Stipules free. ..... 10
2(1). Gynoecium shorter than androecium, often entirely hidden, twigs in innovations 8–12 mm thick, stipules (rufous) villous, stamens 33–39 mm long, filaments 7–8 mm long, gynoecium 24 mm high. ... 12. *Michelia fulva*
2. Gynoecium longer than androecium, twigs in innovations 1–3 mm thick, stipules pubescent, silky, or tomentellous, stamens 7–24 mm long, filaments 1–4 mm long, gynoecium 6–20 mm high. ..... 3
3(2). Leaves minutely (scattered) hairy beneath, connective appendage very long, narrowly triangular, or linguiform. 14. *Michelia kisopa*
3. Leaves with longer hairs beneath, connective appendage triangular. ..... 4

4(3). Gynophore 30 mm long, twigs silky, stipules silky, brachyblast 30–35 mm long, stamens 20–24 mm long. ... 7. *Michelia elliptilimba*

4. Gynophore 2–15 mm long, twigs pubescent, tomentose, or tomentellous, stipules pubescent or tomentellous, brachyblast 3–17 mm long, stamens 7–15 mm long. ... 5

5(4). Reticulation rather obscure. ... 6

5. Reticulation distinct. ... 8

6(5). Pedicle present, twigs tomentellous. ... 20. *Michelia microtricha*

6. Pedicle absent, twigs tomentose. ... 7

7(6). Stipules pubescent, leaf apex shortly acuminate, fruiting brachyblasts 11 cm long, 8 mm thick, fruits 13.5–15.5 cm long, gynophore under fruit 20–25 mm long. ... 23. *Michelia wilsonii*

7. Stipules tomentellous, leaf apex acuminate or acute, fruiting brachyblasts 0.5–0.8 cm long, 3–4 mm thick, fruits 2.5–6 cm long, gynophore under fruit 10–15 mm long. ... 9. *Michelia floribunda*

8(5). Outer tepals 14–30 mm broad, twigs and stipules tomentellous. ... 6. *Michelia doltsopa*

8. Outer tepals 7–9 mm broad, twigs and stipules pubescent. ... 9

9(8). Stipular scars 3–5 mm long, leaves elliptic or narrowly elliptic, brachyblast stout. ... 22. *Michelia velutina*

9. Stipular scars 17–28 mm long, leaves ovate or narrowly ovate, brachyblast slender. ... 3. *Michelia champaca*

10(1). Gynoecium glabrous. ... 11

10. Gynoecium hairy. ... 13

11(10). Plant entirely glabrous. 18. *Michelia maudiae*

11. Plant hairy at least in innovations, stipules pubescent or tomentellous. ... 12

12(11). Petiole 25–30 mm, twigs tomentose, stipules pubescent, reticulation laxly netted, petiole not dilated at base, brachyblast 15–25 mm long, outer tepals 5.5–7 cm long, 15–30 mm broad, stamens 20–25 mm long, gynoecium 17–20 mm high, gynophore 10–20 mm long, fruiting brachyblasts 5–10 mm thick, fruits 7–10 cm long, scars of perianth and stamens along torus under fruit 20–22 mm long, gynophore under fruit 29 mm long. ... 15. *Michelia lacei*

12. Petiole 10–20 mm, twigs puberulous, stipules tomentellous, reticulation densely netted, petiole dilated at base, brachyblast 2.5 mm long, outer tepals 2.3–3 cm long, outer tepals 8–10 mm broad, stamens 8–10 mm long, gynoecium 10–12 mm high, gynophore 2–7 mm long, fruiting brachyblasts 3–3.5 mm thick, fruits 3–6 cm long, scars of perianth and stamens along torus under fruit 4–6 mm long, gynophore under fruit 12–15 mm long. ... 5. *Michelia coriacea*

13(10). Gynophore 10–15 mm long. ... 14

13. Gynophore 2–6 mm long. ... 15

14(13). Gynoecium 3–6 mm high, twigs pubescent, leaves minutely (scattered) hairy beneath, apex shortly acuminate, reticulation distinct, laxly netted, filaments 3 mm long, fruiting brachyblasts 5–7 cm long, fruiting carpels glabrous. ... 17. *Michelia masticata*

14. Gynoecium 17–20 mm high, twigs tomentose, young leaves with longer hairs beneath, apex acuminate or acute, reticulation rather obscure, densely netted, filaments 4–6 mm long, fruiting brachyblasts 1.5–3 cm long, fruiting carpels hairy. ... 10. *Michelia foveolata*

15(13). Outer tepals 1–3 cm long. ... 16

15. Outer tepals 3.2–7 cm long. ... 17

16(15). Leaves minutely (scattered) hairy beneath, twigs and stipules tomentellous, reticulation distinct, pedicle present, connective appendage linguiform, 2–4 mm long, filaments 1.5 2 mm long, gynoecium cylindric, gynophore under fruit 5 8 mm long. ... 19. *Michelia mediocris*

16. Leaves with longer hairs beneath, twigs puberulous, stipules pubescent, reticulation rather obscure, pedicle absent, connective appendage triangular, 0.5–1 mm long, filaments 1 mm long, gynoecium ovoid, gynophore under fruit 10–17 mm long. ... 4. *Michelia compressa*

17(15). Leaves glaucous beneath, twigs villous, stipules silky, gynoecium 20 mm high. ... 13. *Michelia ingrata*

17. Leaves not glaucous beneath, twigs pubescent, tomentose, or tomentellous, stipules pubescent or tomentellous, gynoecium 6–13 mm high. ... 18

18(17). Pairs of lateral nerves 16–18, twigs tomentose, leaf base rounded, inner tepals 10–14, filaments 4 mm long, scars of perianth and stamens along torus under fruit 12–14 mm long. ... 1. *Michelia aenea*

18. Pairs of lateral nerves 10–15, twigs pubescent, or tomentellous, leaf base cuneate or broadly cuneate, inner tepals 6–9, filaments 1–3 mm long, scars of perianth and stamens along torus under fruit 4–7 mm long. ... 19

19(18). Leaves with longer hairs beneath, twigs and stipules tomentellous, leaves elliptic or ovate, outer tepals ovate or spathulate, connective appendage linguiform, gynoecium cylindric. ... 16. *Michelia macclurei*

19. Leaves minutely (scattered) hairy beneath, twigs and stipules pubescent, leaves obovate or narrowly elliptic, outer tepals obovate or elliptic, connective appendage triangular, gynoecium ellipsoid. ... 2. *Michelia cavaleriei*

1. **Michelia aenea** Dandy, J. Bot. 68: 211. 1930. TYPE: *Poilane 12611* (holotype, P; isotype, K).

*Michelia oblongifolia* Chang & B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 3: 86. 1987. TYPE: *B. L. Chen 86S193* (holotype, SYS).

*Michelia longistyla* Law & Y. F. Wu, Acta Bot. Yunnanica 10, 3: 341, t. 7. 1988. TYPE: China. Yunnan: Jinping, 1,800 m, *Q. Wang 142* (holotype, PE not seen).

Tree to 16 m high and 50 cm diam. Indument straight to slightly undulate, usually cupreous, sometimes clear to gray. Young twigs terete, ca.

4 mm diam., purplish brown, densely short-tomentose, glabrescent; old ones dull dark brown, somewhat rough, ± pubescent to glabrous, conspicuously lenticellate and fissured. Stipules densely long-pubescent, free from the petiole. Leaves coriaceous, rigidulous, bright green and glabrous above, pale green, densely appressed-tomentellous below, oblong to narrowly oblong, 18.7–25(–28.5) × 4–6(–7.5) cm; apex shortly acuminate to acute; acumen 3–18 mm; base rounded or obtuse to cuneate or narrowly cuneate; midrib impressed above, prominent below; nerves in 16–18 pairs, anastomosing and meeting in an intramarginal vein, which is slightly more prominent than the fine, densely netted reticulation, inconspicuous above, prominent below. Petiole appressed hairy, glabrescent, slightly thickened toward its base, without scars, 1.3–2.8 cm long. Brachyblasts stout, finely tomentose; spathaceous bracts 2, coriaceous, pubescent outside with same indument as stipules. Flowers white to yellowish; tepals 13–17, the outer 3 obovate, fleshy, 32–35 × 10–12 mm, the inner tepals 10–14, narrowly obovate to spathulate, 21–27 × 5–7 mm; stamens many, 13–16 mm long, connective appendage short-triangular, 0.5–2.5 mm long, filaments yellowish puberulent, ca. 4 mm long; gynoecium ellipsoid, tomentellous, exserted from the androecium, 8–13 mm long; gynophore 2–4 mm long; carpels many, ovoid; ovaries ca. 1 mm long; ovules 8–10; styles ca. 2 mm long. Fruiting brachyblasts pubescent, 3–3.5 cm long, ca. 5 mm wide at the top. Fruits cylindric, 6–10.5 cm long; ripe fertile carpels 4–25, obovoid to ellipsoid, sessile to short-stipitate, 1.4–2.5 × 1–1.5 cm, apically short-beaked; gynophore 1.8–2.5 × 0.4 cm; scars of perianth and stamens along the torus 12–14 × 6 mm. Seeds not seen.

*Distribution.* China and Vietnam. In CHINA. **southeastern Yunnan**: Jinping, Maguan, *Chen B.L. GS 302, Chen B.L. GS 86187.*

*Ecology.* In forests. Altitude: 1,800–1,950 m. Flowering April; fruiting September–October.

*Uses.* Wood very hard and dense, generally used for pillars, planks, and other purposes.

*Collector's note.* Bark rough, slightly brownish.

*Note.* The specimens examined are quite uniform in all characters. There was no material of *Michelia longistyla* available; it is reduced to *Michelia aenea* based on the published description and figure.

2. **Michelia cavaleriei** Finet & Gagnep., Bull. Soc. Bot. France 53: 573, f. 1–8 of t. 1. 1906. TYPE: *Cavalerie & Fortunat 2263* (holotype, P; isotypes, E, K).

*Michelia fallax* Dandy, Notes Roy. Bot. Gard. Edinburgh 16: 130. 1928. TYPE: *Hand.- Mazz. 12281* (holotype, W). [The flowering material collected by Wang Te-Hui is not *M. fallax.*]

*Michelia platypetala* Hand.-Mazz., Akad. Wiss. Wien Math.-Natuurwiss Kl. 58: 89. 1921. TYPE: *T. H. Wang in Hand.-Mazz. 12281* (holotype, W; isotypes, A, K, WU). [Only the flowering material is *M. platypetala.*]

Much branched tree 10–20 m high and 50 cm diam.; bark white-gray; buds, young twigs, stipules, petiole, brachyblasts, and bracts outside densely appressed-pubescent with fine, short to long, straight, clear to brown, glossy hairs; young twigs terete, dull black, 2–3 mm diam., later glabrescent; old ones brownish to brownish gray, smooth or longitudinally fissured, white lenticellate, glabrous to ± pubescent; terminal buds narrowly ovoid, 1–2 cm long. Stipules free from the petiole. Leaves thinly coriaceous, dark green, sparsely scattered-pubescent with short or long, straight or sometimes undulate, clear or brown hairs above, pale green, finely appressed-pubescent with short, straight, clear and brownish hairs, except the midrib beneath soon glabrescent, narrowly elliptic or obovate-elliptic, (10–)12–20(–24) × 3.5–5.5(–7) cm; apex short-acuminate, acumen 7–20 mm long; base cuneate to broadly cuneate; midrib conspicuously prominent below, ± impressed above; nerves fine, visible on both sides, in 11–15 pairs, reticulation fine, closely netted. Petiole ca. 1.5–3 cm long, without stipular scars. Flower buds narrowly ovoid, 2–3 cm long; brachyblasts 5–15(–25) mm long, 3–5 mm wide at the top, pedicles 0–2 mm long; bracts 3–4. Tepals 9–12, white, the outer 3–4, obovate-elliptic, 4.5–5.6(–7) × 2–2.5 cm, the inner tepals narrowly obovate to spathulate; stamens 7–15 mm long, connective appendage triangular, ca. 1 mm long, filaments 2–3 mm long, ca. 1 mm wide; gynoecium ellipsoid, tomentellous, 6–10 mm long, slightly protruding from the androecium; gynophore tomentellous, 4–5 mm long, ovaries ovoid, 1.5–2.5 mm long; ovules ca. 10; styles glabrous, 1.5–3 mm long. Fruits 5–15 cm long; ripe carpels 6–14 (some carpels abortive), ovoid to obovoid, dark brown, smooth to lenticellate, short-stipitate to sessile, with short beaks at the apex, 13–25 × 7–13 mm; gynophore 10–25 × 2–3 mm; torus with the scars of perianth and stamens 5–7 × 5–6 mm. Seeds 1–4 in each carpel, ellipsoid to subcordate, 5–9 × 6–8 mm.

*Distribution.* CHINA. **Fujian**: Nanjung Xian, *Ye. G.D. 1301.* **Guangdong**: Tou Che Swi, Yuyuen, *Kwok S.P. 80166.* **Guangxi**: Damiaoshan, *Lu Q.H. 3526*; Guan Xian, *Chen Z.Z. 52664*; Lingui, *Deng X.F. 201*; Longsheng, *Long Sheng Exped. 50416*; Nandang, *Cai C.X. 77- 2*; Tianlin, *Li Y.K. 591*; Yanshan, *Liang J.Y. 100312*; Chuen Yuen, *Tsoong C.H 82048*; Ling Yun Hsien, *Steward A.N. & Cheo, H.C. 23*; Ziyuan, *Huang Z.F. 20.* **Guizhou**: Leishan Xian, *Jiang R.B. 13*; Fanjinh Mt., *Sino-British Exped. 37*; *Jiankou Xian, Sino-American Guizhou Bot. Exped. 396*; Songtao Xian, *Sino-American Guizhou Bot. Exped. 1983.* **Hunan**: Qianyang, *Li Z.T. 1708*; Sheng, Xinning Xiang, Ziyu Shan, *Li Zhen-yu et al. 1899*; Wugang, *Lin Q.Z. 10435.* **Hubei**: Lichuan, *Tang G.G. 679.* **Sichuan**: Fanchingshan, *Du D.H. 3854.* **Yunnan**: Fengging, *Zhu T.P. 554*; Yuanyang, *He S.C. 85170*; Pin-fa, *Cavalerie J. 7312.*

*Ecology.* In forest. Altitude: 800–1,500 m. Flowering March; fruiting September–October.

*Collector's note.* Trees in mixed forests on rock or open area on riverbank; flowers white, fragrant, gynoecium hairy, extending outside androecium; fruits greenish or brownish; seeds reddish to red.

3. **Michelia champaca** L., Sp. Pl.: 536. 1753. *Michelia rheedii* Wight, Ill. Ind. Bot. 1: 13. 1840. TYPE: *Hermann Fl. Zeyl. 144* (holotype, BM).

*Michelia euonymoides* N. L. Burm., Fl. Ind.: 124, 1768. *Sampacca sylvestris* Rumph. SYNTYPES: *Hb. Burmann 15 & 55* (L).

*Michelia suaveolens* Pers., Syn. Pl. 2: 94. 1806. *Michelia blumei* Steudel, Nomencl. ed. 2, 2: 139. 1841. *Michelia tsiampacca* var. *blumei* Moritzi in Zoll., Syst. Verz.: 36. 1846. *Sampacca suaveolens* O. Kuntze, Rev. Gen. Pl. 1: 6. 1891. TYPE: Rumph., Herb. Amboin. 2: t. 67. 1741.

*Michelia tsiampacca* Blume, Bijdr.: 7. 1825, non *Michelia tsiampacca* L. 1767. *Michelia velutina* Blume, Fl. Javae Magnoliaceae: 17. 1829, non *Michelia velutina* DC., 1824, *Champacca velutina* O. Kuntze, Rev. Gen. Pl. 1: 6. 1891. *Michelia pilifera* Bakh. f., Blumea 12: 61. 1963. TYPE: *Blume s.n.* (holotype, L, sheet no. 908.126-1868; isotypes, K, NY).

*Michelia pubinervia* Blume, Fl. Javae Magnoliaceae: 14, t. 4. 1829. *Michelia rufinervis* Blume, Bijdr.: 8. 1825, non *Michelia rufinervis* DC., 1817. *Michelia champacca* var. *pubinervia* (Blume) Miq., Ann. Mus. Bot. Lugduno-Batavum 4: 72. 1868. TYPE: *Blume 670* (holotype, L; isotypes, B, K).

*Talauma villosa* Miq. forma *celebica* Miq., Ann. Mus. Bot. Lugduno-Batavum 4: 70. 1868. TYPE: *De Vriese & Teijsmann s.n.* (holotype, BO).

*Magnolia champaca* Baillon ex Pierre, F. Forest. Cochinch.: t. 3. 1880. TYPE: *Herb. Pierre 187.* (?)

*Magnolia membranacea* P. Parm., Bull. Sci. France Belgique 27: 200, 258. 1895. SYNTYPES: Mauritius, *Sieber III* (K, L, MEL), *Sieber 156* (MEL, P), locality unknown, *D.J. Anderson*, 1868 (MEL).

Tree to 30–40 m high and 1 m diam.; indument composed of short, straight or slightly undulate, appressed or erect, clear to yellow, rarely brownish hairs; young twigs 2–3 mm diam., brown-gray, pubescent, glabrescent; old ones gray to black-brown, ± lenticellate. Stipules pubescent, adnate to the petiole from about half of its length to nearly to the top, scars 1.7–2.8 cm long. Leaves thinly coriaceous, green, above glabrous, or at first especially on the midrib sparsely pubescent, later glabrescent, beneath paler green, pubescent, glabrescent, ovate-oblong to narrowly ovate, 8–23(–34) × 3.4–9(–12) cm; apex acute to gradually long-acuminate; base attenuate to cuneate or more often rounded; midrib ± impressed above, prominent below, nerves fine, visible on both sides, more prominent below than above, in 11–22 pairs. Petiole pubescent, glabrescent, 2–3.2(–4.5) cm long. Flowers very fragrant; bud ovoid to ovoid-ellipsoid; bracts 3 or more rarely 4, tomentellous or pubescent outside; brachyblast usually slender, 7–12 × 2–3 mm, tomentose or densely pubescent, pedicles 0–1 mm long. Tepals 12–15(–21), yellow to orange, subsimilar, glabrous or pubescent outside at the base; the outer 4–6 narrowly obovate, narrowly obovate-linear, to spathulate, 20–40 × 7–9 mm; stamens 7.5–8 mm long, connective appendage short-triangular, 0.5–1 mm long, filaments 1.5–2 mm long; gynoecium ovoid-cylindric, 7–12 mm long; gynophore tomentellous, 3–5 mm long; carpels ca. 30, tomentellous; scars of perianth and stamens along torus 1–2 mm long. Fruiting brachyblast glabrescent, gray-brown, 10–30 × 3–5 mm. Fruit 2–15 cm long; ripe carpels 4–19 or more, ovoid to ellipsoid, densely lenticellate, glabrescent, 10–20 × 7–11 mm, sessile and without a beak. Seeds subcordate, ellipsoid to irregularly shaped, 9–10 × 6–8 mm, 2–4 in each carpel.

*Distribution.* India, China, Burma, Vietnam, and Malesia. In CHINA. **Southern and southwestern Yunnan**: Che-li Hsien, *Wang C.W. 77767*; Fo Hai, *Wang C.W. 73905*; Jengyueh, 25°N, 98°36′E, *Forrest G. 25302.* Southeastern Xizang. Cultivated in Guangdong, Hainan, and Giangxi.

*Ecology.* In forests. Altitude: 650–1,600 m. Flowering June–July; fruiting September–October.

*Uses.* Wood used for furniture and ships; the flowers and leaves are extracted for volatile oil; the tree is grown as an ornamental.

*Collector's note.* Flowers ivory yellow to yellow, strongly fragrant.

*Note.* De Candolle (1817, 1824), Decaisne (1835), Spanoghe (1841), Moritzi in Zollinger

(1846), and Miquel (1858) misspelled the name as *Michelia tsiampacca* (auct. non L., 1797).

For further misapplied names and nomina nuda see Nooteboom (1985).

4. **Michelia compressa** (Maxim.) Sarg., Forest Fl. Japan. 4: 75, 77, t. 13. 1893. *Magnolia compressa* Maxim., Bull. Acad. Imp. Sci. Saint-Petersbourg 17: 417. 1872. TYPE: Yagami, near Nagasaki, Hizen Prov., Kiushu, *Maximowicz*, 1862 (holotype,?; isotype, BM).

*Magnolia philippinensis* P. Parm., Bull. Sci. France Belgique (Parmentier) 27: 206, 270. 1895. *Michelia philippinensis* (P. Parm.) Dandy, Kew Bull. 1927: 263. 1927. *Michelia cumingii* Merr. & Rolfe, Philipp. J. Sci. 3 Bot.: 100. 1908. TYPE: *Cuming 783* (holotype, MEL; isotypes, A, BM, K, L, NY).
*Michelia compressa* var. *formosa* Kanehira, Trans. Nat. Hist. Soc. Taiwan 20: 384. 1930. *Michelia formosana* (Kanehira) Masamune & Suzuki, Annual Rep. Taihchu Bot. Gard. 3: 57. 1933. *Michelia taiwaniana* Y. W. Law, Iconogr. Cormoph. Sinicorum 1: 796, t. 1592. 1972, nomen illeg. *Michelia iteophylla* C. Y. Wu ex Law & Y. F. Wu, Acta Bot. Yunnanica 10, 3: 337, t. 7. 1988. TYPE: *Lo 1359* (holotype, KUN).

Small tree, 8–12 m high; young twigs terete, slender, 1–2 mm diam., dull brownish to dark black-brown, smooth and appressed-puberulent with short, straight, clear, brown to rufous hairs; old ones purple-brown, glabrescent, sparsely lenticellate; terminal buds obovoid to cylindric, 8–11 mm long, densely appressed-pubescent with gray or rufous, glistening hairs. Stipules pubescent, free from the petiole. Leaves chartaceous to coriaceous, glabrous on both surfaces, or at first sparsely pubescent with long, straight and slightly undulate hairs on both sides, or below, especially on the midrib and toward the base, densely hairy with long, straight, erect, rufous hairs, finally glabrescent, elliptic to narrowly elliptic, 4–12 × 1.5–3.5 cm; apex acute to acuminate, acumen 1–15 mm long, sometimes obtuse and occasionally slightly emarginate, base cuneate, rarely obtuse and often slightly unequal; midrib slightly impressed above; nerves in 8–15 pairs, obscure, slightly more prominent than the rather fine reticulation below, reticulation densely netted. Petiole slender, glabrous or with same indument as young twigs, without stipular scars, 5–22 mm long. Brachyblast tomentellous with gray to brown hairs, 3–6 × 1.5–3 mm, pedicle absent; bracts 2–3, pubescent outside as are terminal buds. Flower white to creamy yellow, much scented; tepals 9(–14), subsimilar, the outer 3 oblanceolate to oblanceolate-linear, mostly broader than the inner tepals, 10–28 × 3–10 mm; stamens many, 2.5–7 mm long, connective appendage triangular, 0.5–1 mm long, filaments ca. 1 mm long; gynoecium ovoid to ovoid-oblong, tomentellous, 4–6 mm long, much longer than the androecium; gynophore with same indument as gynoecium, 2–6 mm long; carpels 5–13 or more, ovaries ca. 1.8 mm long; styles ca. 0.2 mm long; ovules 2–8. Fruiting brachyblast gray hairy, 3–8 × 1.5–8 mm. Fruit 5–7 cm long; ripe carpels 1–12 or more, ovoid to ellipsoid, dark brown, sessile or with a ca. 2–9-mm-long stipe, sparsely white-lenticellate, apically short-beaked, 11–15 × 8–14 mm; gynophore ± pubescent, 10–17 × 2–4 mm; torus with the scars of perianth and stamens, 2–3 × 2.5–6 mm. Seeds 1–2, subcordate, ellipsoid to irregularly shaped, 7–9 × 6–7 mm.

*Distribution.* China, the Philippines, and southern Japan. In CHINA. **Taiwan**: Taihokushy, *Sasaki S. 93*; Taipei, Kankou, *Hsu C.C. & M.T. Kao K 3680*; Bon Bon, I Lan, *Liao Jih-Ching 10006*; Botel Tobago, *Chang C.E. 3651*; Henchun Peninsula, *Chang C.E. 3289*. Also eastern and southern Yunnan.

*Ecology.* In forest. Altitude: 200–2,600 m. Flowering, fruiting January.

*Uses.* Wood straight-grained, fine-textured, heavy and hard, used for building, furniture, ships, woodcarving, and other purposes.

*Note.* After comparative studies of collections of all the cited synonyms from Japan, China, and the Philippines, we came to the conclusion that they all belong to a single species: *Michelia compressa* is the most widely distributed species of the genus.

It is noteworthy that *Michelia compressa* shows much variation throughout its area in size of the flowers, number of carpels and ovules, as well as length of the stipe of the ripe carpels. The flowers are smaller in the specimens of the Philippines, larger in Taiwan and Japan. Both carpels and ovules from Taiwan and Japan are slightly more in number than from the Philippines. The length of the stipe of the follicles varies from 0 to 8 mm. These variations can be observed even in the same specimen.

Gagnepain (1929) named this species *Michelia figo* (auct. non Loureiro, 1790). Merrill (1906) used the name *Michelia parviflora* (non DC., 1817).

5. **Michelia coriacea** Chang & B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni 3: 89. July 1988. TYPE: *B. L. Chen & B. Li GS 9035* (holotype, SYS). Figure 9.

FIGURE 9. *Michelia coriacea* Chang & B. L. Chen.—1. Fruiting branch.—2. Seed.—3. Seeds with testa removed. Based on *SYS 161742 = Chen Bao Liang GS 9035*. Drawing by Xie Qing Jian.

FIGURE 10. *Michelia doltsopa* Buch.-Ham. ex DC.—1. Fruiting branch.—2. Flower. Based on *SYS 161753* = *Chen Bao Liang 86 S 049*. Drawing by Xie Qing Jian.

*Michelia polyneura* C. Y. Wu ex Law & Y. F. Wu, Acta Bot. Yunnanica 10(3): 340, f. 1–8 of t. 5. Aug. 1988. TYPE: *K. M. Feng 12030* (holotype, KUN; isotype, A).

Tree 10–18 m high and 20–45 cm diam.; young twigs dull brown, 3–7 mm diam., ± gray puberulent; old ones dark brown, glabrescent, with sparse orbicular and white lenticels; terminal buds ovoid, densely tomentellous with short, straight, clear, gray to brownish hairs. Stipules with same indument as the terminal buds, free from the petiole. Leaves coriaceous, green, glossy above, pale green

beneath, both surfaces glabrous, oblong to broadly elliptic, sometimes obovate, often unequal, 9.7–13.9(–16.1) × 2.2–3.6(–6) cm; apex acute to acuminate, acumen 5–10 mm long, base cuneate or rounded; midrib slightly impressed above, rather prominent beneath; nerves in 12–13(–16) pairs, much visible on both sides, curved upward and meeting in an intramarginal vein, all lesser veins forming together a dense reticulation that is prominent on both surfaces, the larger alveoli filled with the smaller veins, which are obvious to obscured. Petiole glabrous, dilatate toward the base, 1–2 cm long. Brachyblast tomentose, 2.5 mm long (mature flowers not seen). Flower buds ellipsoid, tepals 9, white, subsimilar, obovate to narrowly obovate, 2.3–3 × 0.8–1 cm; stamens ca. 80, 8–10 mm long, connective appendage narrowly triangular, 1.5–2 mm long, filaments 2.5–3 mm; gynoecium glabrous, subcylindric, exserted from the androecium, 1–1.2 cm long; gynophore 2–7 mm long. Fruiting brachyblasts yellowish pubescent, with 3 scars of bracts, 8–25 × 3–3.5 mm, pedicles absent or very short, ca. 1.5–2 mm long if present. Fruits 3–6 cm long with 1–4(–10) fertile carpels and 6–8(–17) abortive carpels, the ripe carpels sessile, ovoid, dull and dark brown, conspicuously lenticellate, 18–25 × 12–17 mm; gynophore 1.2–1.5 cm long, scars of perianth and stamens along 4–6 mm of the torus. Seeds ellipsoid, smooth, 10–11 × 6–7 mm.

*Distribution.* CHINA. **Southeastern Yunnan**: Guangnan, *Wang C.W. 88023*; Malipo, *86915*; Si Chour Hsien, *Feng K.M. 12030.*

*Ecology.* In forests, on limestone formations. Altitude: 1,450 m. Flowering April; fruiting September–October.

*Note.* The type of *Michelia coriacea* bears fruits. In the absence of flowers, we misrepresented the tepals as 6–7 in number, based on the faint scars of the perianth on the torus. The collections with flowers collected from the same tree one year later showed that the flower has 9 tepals.

6. **Michelia doltsopa** Buch.-Ham. ex DC., Syst. Nat. 1: 448. 1817. TYPE: *Buchanan-Hamilton s.n.* (holotype, BM). Figure 10.

*Michelia excelsa* (Wall.) Blume, Fl. Javae Magnoliaceae: 9. 1829. *Magnolia excelsa* Wall., Tent. Fl. Nepal.: 5, t. 2. 1824. *Sampacca excelsa* (Blume) Kuntze, Revis. Gen. Pl. 1: 6. 1891. TYPE: *Wallich 6494* (holotype, K; isotypes, BM, NY).

*Michelia calcuttensis* P. Parm., Bull. Sci. France Belgique (Parmentier) 27: 283. 1895. TYPE: Type specimen not traced. According to P. Parm., its label said: "Michelia ?Assam. ex herb. hort. bot. calcuttensis."

*Michelia manipurensis* G. Watt ex Brandis, Indian Trees: 8. 1906. TYPE: *G. Watt 6329* (K).

*Michelia wardii* Dandy, Kew Bull. 1929: 222. 1929. TYPE: *F. Kingdon Ward 8060* (holotype, K).

*Michelia opipara* Chang & B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 3: 90. 1987. TYPE: *B. L. Chen GS86237* (holotype, SYS).

Tree or rarely a shrub, to 30 m high; buds appressed-rufous or gray tomentellous, later glabrescent; young twigs 2.5–3 mm diam., sparsely tomentellous, glabrescent, brownish to dull black-brown. Stipules appressed-rufous or gray tomentellous, adnate to the petiole, scars 2–6(–20) mm long. Leaves chartaceous to thinly coriaceous, green, olive green to brown when dry, above scattered-pubescent with slender, straight to undulate, clear hairs, glabrescent, beneath pale green to glaucous, appressed-tomentose with short or long, straight to occasionally undulate, usually rufous, sometimes clear to brownish hairs, elliptic, oblong-elliptic, oblong to narrowly ovate-elliptic, usually ± unequal, 9–22 × 4–8 cm; apex acuminate or subacuminate, acumen 1–3 cm long, base broadly cuneate or rounded, the margin slightly wavy; midrib impressed above, prominent below, nerves prominent below, in 10–14 pairs, reticulation fine, densely netted. Petiole pubescent, glabrescent, 0.8–2.5 cm long. Brachyblasts densely appressed-rufous to gray tomentose, 4–13(–23) × 4–6 mm, pedicles 2–5 mm long; bracts 2–3(–5), densely rufous tomentose. Flowers with pleasant smell; buds ovoid to oblong, 4–5 cm long; tepals (8–)12–16, white to yellow, the outer 4–5 obovate to spathulate-obovate or oblanceolate, 3.7–7.5 × 1.4–3 cm, glabrous to pubescent outside toward the base; stamens 8–15 mm long, connective appendage short to long triangular, 1–3 mm long, filaments 2–3 mm long; gynoecium subcylindric, 1–2 cm long, exserted from stamens; gynophore 5–12 mm long, tomentellous; carpels many, subovoid, ca. 1.5 cm long, appressed-tomentellous; styles glabrous; scars of perianth and stamens on torus 4–6 mm long. Fruiting brachyblasts glabrous or ± pubescent, 9–13(–23) × 4–7 mm. Fruits (2–)5–12.5 cm long, some carpels abortive; ripe carpels sessile or substipitate, 10–15 × 8–12 mm; gynophore 10–22 × 2–4 mm, scars of perianth and stamens under fruit 7–10 × 4–7 mm. Seeds ovoid to ellipsoid, 8–11 × 8 mm.

*Distribution.* Nepal, Bhutan, northeastern India, China, and northern Burma. In CHINA. **Southern Xizang**: *Kingdon Ward F. 19299, 19211.* **Yunnan**: Shweli-Salwin divide, 24°20′, *Forrest G. 8949*; Jinping, *Sino-Rossica Yunnan Exped. 1532*; Mienning, Poshang, *Yu T.T. 18055*; Shange-pa, *Tsai H.T. 58995*; Shunning, Hila, Wumulung, *Yu T.T. 16662*; Taron-Taru divide, *Yu*

*T.T. 20866*; Yengyueh, 25°25′N, 98°30′E, *Forrest G. 26258*.

*Ecology.* In broad-leaved forest. Altitude: 1,600–2,400 m. Flowering April–May; , fruiting September–October.

*Uses.* Wood light, soft, fine-textured, very durable and easily workable; used for various objects of construction work and carpentry, as well as for planking, doors, window frames, and furniture.

*Collector's note.* Flowers pale yellow or white, fragrant.

*Note.* See Dandy (1927b). *Michelia opipara* is similar to *Michelia doltsopa* except for its gray to yellowish indument. The former name is therefore reduced to a synonym of the latter.

7. **Michelia elliptilimba** B. L. Chen & Nooteboom, sp. nov. TYPE: China. Yunnan: Meng-hua, Chukai, alt. 2,000 m, 12 May 1938, *T. T. Yü 15854* (holotype, A; isotypes, E, IBSC). Figure 11.

Arbor 5 ad 6 m alta, ramunculis, stipulis extra, foliis utrinque, petiolibus, brachyblastis, bracteis, gynophoris, ovariisque indumento pilis tenuibus parvis vel longis, undulatis, brunneis. Ramunculi 2–3 mm diametro. Stipulae petiolis 2–2.5 cm longis cicatricibus 3–4 mm longis adnatae. Folia elliptica ad ovato-elliptica 16 ad 22 cm longa, 7.5 ad 10 cm lata apicibus acutis vel acuminatis basibus obtusis glabrescentia, glaucescentia, nervis primariis 9–14 paribus dense reticulata. Brachiblasti 3 ad 3.5 cm longi cicatricibus bractearum 3 ad 4. Flores pedicello 5 ad 7 mm longo, tepalis exterioribus 3, obovatis, 5.5 ad 6.5 cm longis, tepalis interioribus 8, obovatis ad spathulatis, ca. 5.7 cm longis, staminibus 20 ad 24 mm longis, gynaecio cylindrico 15 mm longo gynophoro 30 mm longo et 6 mmm lato.

Tree 5–6 m high; bark greenish gray, smooth; young twigs, stipules outside, leaves on both sides, petioles, brachyblasts, bracts, gynophore, and ovaries covered with fine, short or long, undulate, brownish to brown hairs. Young twigs 2–3 mm diam., old ones ± hairy or glabrous; terminal buds ca. 15 mm long; stipules adnate to the lower bases of the petiole, stipular scars 3–4 mm long. Leaves thinly coriaceous, green above, glabrescent and becoming glaucous beneath, elliptic to ovate-elliptic, 16–22 × 7.5–10 cm; apex acute or acuminate, base obtuse; midrib impressed above, conspicuously prominent below, nerves visible on both sides, more prominent beneath than above, in 9–14 pairs, reticulation closely netted, prominent on both sides. Petiole 2–2.5 cm long. Flowers creamy white, with a pleasant scent; brachyblasts with 3–4 scars of bracts, 3–3.5 cm long, 5–6 mm wide at the base, pedicles 5–7 mm long; tepals 11–12, subsimilar, the outer 3 obovate, attenuate toward the base, short-clawed, 5.5–6.5 × 2.5–3 cm, the inner tepals 8, obovate to spathulate, ca. 5.7 × 1.5–2 cm; stamens 20–24 mm long, connective appendage triangular, ca. 0.5 mm long, filaments 2–4 mm long; gynoecium cylindric, much longer than the androecium, ca. 15 mm long; gynophore ca. 30 × 6 mm; carpels many, ovaries ovoid, 4–5 mm long; styles glabrous, 2.5–3 mm long. Fruits not seen.

*Distribution.* CHINA. **Yunnan**: Meng-hua, Chukai, *T. T. Yü 15854*.

*Note.* This species resembles *Michelia baillonii* in the vegetative characters except in its glaucous lower leaf surface. The flowers, however, are very similar in size and shape to those of *Michelia foveolata*. Only one collection available.

8. **Michelia flaviflora** Law & Y. F. Wu.

See under dubious species.

9. **Michelia floribunda** Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 46, f. b of t. 7. 1905. TYPE: *Bons d'Anty 30* (holotype, P; isotypes, K, E).

*Michelia kerrii* Craib, Kew Bull. 1922: 166. 1922. TYPE: *Kerr 4679* (holotype, K; isotypes, BM, K, P, UC).

Tree to 28 m high and 1 m diam.; bark gray; young twigs slender, 1.5–2 mm diam., brown or purple-brown to purple-black, at first tomentose with short or long, straight, glistening, brown, yellowish to gray hairs, soon glabrescent. Stipules appressed-tomentellous with same hairs as young twigs, adnate to the petiole, stipular scars 2–14 mm long, sometimes to 2.2 cm long. Leaves thinly coriaceous to coriaceous, dark green, glossy, at first sparsely appressed-pubescent with slender, clear hairs, especially on the midrib, later glabrescent above, glaucous or not, appressed-pubescent with long to rather long, straight, clear, brown, rarely dark brown hairs, glabrescent beneath, narrowly elliptic, narrowly obovate-elliptic, ovate-elliptic, oblong-elliptic to narrowly ovate; 6–14.5(–17) × 1–4.5(–5) cm; apex acute to acuminate, sometimes ± caudate, acumen 5–15 mm long, occasionally to 2 cm long, base cuneate or rounded; midrib impressed above, nerves fine, obscure on both sides, more prominent beneath than above, in 8–14 pairs, reticulation fine and dense, hardly visible on both sides. Petiole appressed-tomentellous or pubescent, 9–25(–40) mm long. Brachyblast covered with same indument as young

FIGURE 11. *Michelia elliptilimba* B. L. Chen & Noot.—1. Branch with deflorated flower.—2. Flower.—3. Stamen.—4. Follicle. Based on *T. T. Yü 15854* (A). Drawing by Joop Wessendorp, Rijksherbarium, Leiden.

twigs, 3–6(–8) × 2.5–4 mm, pedicle absent; bracts 3(–4), brown or silver sericeous outside. Flower bud ovoid to cylindric, 2–4.4 cm long; flower fragrant; tepals 12–15, outer tepals 3, white, subsimilar, glabrous to puberulent outside toward the base, spathulate, broadly obovate, obovate-linear, rarely narrowly rhombic, tapering toward the base, usually basally with short or long claw, 19–45(–50)

× 6–18(–23) mm; stamens 7–11 mm long, connective appendage short- or long-triangular, 1–3 mm long, filaments ca. 2 mm long; gynoecium cylindric, longer than the androecium, 9–14 mm long; gynophore brown to gray tomentellous, 3–15 mm long; carpels tomentellous; styles glabrous; ovules 3–8 in each carpel; torus with scars of perianth and stamens 2–6 × 3–5 mm. Fruiting brachyblast pubescent, 5–8 × 3–4 mm. Fruit 2.5–6 cm long, contorted; ripe carpels 1–14, subglobose, brown to dark brown, lenticellate, ± puberulent, apically beaked, 7–20 × 8–14 mm. Scars of perianth and stamens 3–5 × 3–4 mm. Gynophore under fruit pubescent, 1–1.5 cm. Seeds ellipsoid, cordate to irregularly shaped, 6–8 × 5–6 mm.

*Distribution.* China, Thailand, Vietnam, Laos, and Burma. In CHINA. **Guangxi**: Jinxiu Xian, *Da Yao Shan Exped. 10756.* **Hubei–Sichuan**: Metaseqoia area, *Hwa C.T. 503*, **Jiangxi**: *Gongda 740250.* **Guizhou**: Fan Ching Shan, *A.N. & Cheo, H.C. 870*; Yinkiang, *Tsiang Y. 7589.* **Sichuan**: Guan Xian, *Yi G.P. 76002*; Pei Pah, *Law Y.W. 306.* **Yunnan**: Ma Chang Kai valley, *Forrest G. 9460*; Mienning,Poshang, *Yu T.T. 17894*; Chen kang hsien, *Wang C.W. 72551*; Si Chou Hsien, *Wang C.W. 85542*; Tengyueh, *Rock J.F. 7933*; Szemao, *Rock J.F. 2766.*

*Ecology.* In forests. Altitude: 800–2,700 m. Flowering February–June; fruiting July–October.

*Collector's notes.* Flowers white to creamy yellow; fruits green, with red fleshy seeds.

*Note.* The ranges of both *Michelia doltsopa* and *Michelia floribunda* overlap in western Yunnan. Some collections are difficult to identify and probably are hybrids.

L. Diels. (1912, 1913) and Hu in Hu & Chun (1929 pro parte) erroneously dealt with this species under *Michelia wilsonii* (auct. non Finet & Gagnep. 1905). Craib (1925a) named it *Michelia manipurensis* [auct. non Watt ex Brandis. 1906: *Kerr 4926* (BM, E, K)].

10. **Michelia foveolata** Merr. ex Dandy, J. Bot. 66: 360. 1928. TYPE: *W. T. Tsang & K. C. Wong 2738* (in *C. C. C. 14599*) (holotype, UC; isotype, SYS).

*Michelia fulgens* Dandy, J. Bot. 68: 210. 1930. TYPE: *Poilane 7092* (holotype, P; isotype, K).

*Michelia foveolata* var. *cinerascens* Law & Y. F. Wu, Bull. Bot. Res. (China) 6, 2: 99. 1986. TYPE: China. Zhejiang: Qingyuan Xian, *X. Wu 7720* (holotype, IBSC not seen).

Tree to 45 m high and 90 cm diam.; bark pale gray or dark gray; young twigs yellow or brown, appressed-tomentose with short, straight, glossy, clear to yellowish or brown hairs; old ones purple-brown, ± pubescent, lenticellate. Stipules brown tomentose or sericeous, free from the petiole. Leaves coriaceous, rigid, above dark green, glossy, appressed-pubescent with slender, straight, brown (when young) to clear (when old) hairs, especially on the midrib, below appressed-tomentose with short, straight, silver to brown hairs, glabrescent, considerably variable in shape and size, narrowly to broadly obovate, obovate-elliptic, narrowly obovate-elliptic to elliptic-oblong, 9.5–26 × 4.5–12.5 cm; apex acute to acuminate, base cuneate or obtuse to rounded, sometimes nearly cordate, ± oblique; midrib impressed above, prominent beneath, nerves visible on both sides, in 12–16 pairs, reticulation dense, seemingly foveolate, obscure on both sides. Petiole tomentose, glabrescent, 1.5–3.5 cm long, without scars. Brachyblast tomentose with same indument as young twigs, 13–25 × 4–7 mm, pedicle absent; bracts 3–4(–5), densely brown sericeous outside. Flower bud oblong, ca. 3.7 cm long; flower fragrant; tepals 9–12, white or greenish white, subsimilar, broadly obovate to spathulate, 3–4.5 × 1.6–2.4 cm, pubescent toward the base; stamens 17–20 mm long, connective appendage rather short, ca. 0.5 mm long, filaments 4–6 mm long; gynoecium cylindric, exserted from stamens, 1.7–2 cm long; gynophore tomentose with silver to yellow hairs, 1.2–1.5 × 0.2 cm; carpels many, tomentose with the same hairs as gynophore; ovules 10 or more; scars of perianth and stamens along torus ca. 3 × 3 mm. Fruiting brachyblast 15–30 × 4–7 mm. Fruit 5.5–14 cm long; ripe carpels 2–12, subglobose, obovoid, black-brown, ± pubescent, lenticellate, stipitate to short-sessile, beaked, 8–22 × 7–14 mm; gynophore tomentose, 17–30 mm long; scars of perianth and stamens 5–7 × 4–5 mm. Seeds subglobose to ellipsoid, 7–8 × 5–7 mm.

*Distribution.* Vietnam, China. In CHINA. **Guangdong**: *Chun W.Y. 7179.* **Guangzhou**: Ah Po Shan, *Taam Y.W. 572*; Chang Ki Tong, Shi Shan, Yuyuen, *Kwok S.P. 80335*; Kook Kiang, *Ko S.P. 50410*; Lok Chong, *Tso C.L. 20354.* **Guangxi**: Dayao Shan, *Li Z.Q. 99*; Debao, *Li Z.T. 604032*; Jinxui Xian, *Da Yao Shan Exped. 11080*; Lingui, *Liang C.F. 31751*; Longshen, *Zhang, B.N. 406132.* **Guizhou**: Jiangkou Xian, *Sino-American Guizhou Bot. Exped. 1077*; Xingren Xian, *Dang C.Z. 1618.* **Hainan**: Bak Sa, *Lau S.K. 26589*; Baoting, *Hainan Exped. 752*; Fan Yah, *Chun N.K. & C.L. Tso 44233*; Hung Mo Shan, *McClure F.A. (LU 18302) 768*; Miu Tsuen, *McClure F.A. (LU 18246) 712.* **Hunan**: *Tam P.C. 62498.* **Yunnan**: Malipo, *Law Y.W. 7066*; Pingpien, *Mao P.I. 4253*; Xichou, *Liu Y.A. 101762.* Also reported from Fujian, Jiangxi, and Zhejiang.

*Ecology.* In evergreen broad-leaved and mixed forest. Altitude: 500–1,800 m. Flowering March–April; fruiting September–November.

*Uses.* Wood straight-grained and fine-textured, suitable for building, furniture, and plywood.

*Collector's notes.* Fairly common, flowers white or yellow; fruits greenish, light gray, or purplish red.

*Note.* *Michelia foveolata* is a recognizable species. However, the shape and size of the leaves and color of the indument varies.

11. **Michelia fujianensis** Q. F. Zheng.

See under dubious species.

12. **Michelia fulva** Chang & B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 3: 87. 1987. TYPE: *B. L. Chen GL86-193* (holotype, SYS). Figure 12.

Tree to 15 m high and 15 cm diam.; buds, young twigs, stipules outside, leaves beneath, petiole, brachyblasts, and bracts outside densely appressed-hispid with short to long, straight to undulate, somewhat glistening, fulvous hairs; young twigs 8–12 mm diam., dull brown, rough; old ones provided with lenticels, longitudinally fissured. Stipules adnate to the base of the petiole, stipular scars 7–10 mm long. Leaves coriaceous, rigid, bright green, above glabrous to ± pubescent, below pale green to glaucous, glabrescent when old, elliptic, ovate, obovate to oblong, (14–)18–24(–29) × 7–10(–12) cm; apex acuminate to acute, base cuneate, sometimes rounded; midrib impressed above, much prominent beneath; nerves in 7–11(–14) pairs, meeting in a looped intramarginal vein; reticulation densely netted, both nerves and reticulation prominent on both sides. Petiole stout, dilatate toward the base, 2–3 cm long. Brachyblast 2–2.2 × 1–1.2 cm, pedicle absent; spathaceous bracts 2–3, broadly elliptic, ca. 52 × 21 mm. Flower bud long ovoid, ca. 3.7 × 2 cm; tepals 12–13, white, subsimilar, fleshy, obovate to elliptic, the inner tepals smaller than the 3 outer ones, 4.4–5.3 × 2–3 cm; stamens ca. 146, 33–39 mm long, filaments 7–8 mm, anthers 25–30 mm, connective appendage short-triangular, ca. 1 mm; gynoecium cylindric, ca. 24 mm long hidden within and much shorter than stamens; gynophore pubescent, ca. 6 mm long; carpels ca. 152, fulvous pubescent, ovaries 2–3 mm long; styles glabrous, 1–2.5 mm long, scars of perianth and stamens on torus ca. 10 mm long. Ripe carpels ovoid, sessile, 10–15 × 9–10 mm.

*Distribution.* CHINA. **Yunnan**: Maguan, *B. L. Chen GL86-193.*

*Ecology.* In forest on limestone formations. Altitude: 1,690 m. Flowering April.

*Collector's note.* The natural color of the tepals is not known precisely because the flowers collected seemed nearly dry.

*Note.* The distinguishing characters of this species are: plant covered with fulvous hispid hairs; leaves large and rigid, pale green to glaucous beneath; flowers quite big.

13. **Michelia ingrata** B. L. Chen & S. C. Yang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 3: 95. July 1988. TYPE: *B. L. Chen & C. N. Mai 87 T 019* (holotype, SYS). Figure 13.

*Michelia calcicola* C. Y. Wu ex Law & Y. F. Wu, Acta Bot. Yunnanica 10, 3: 339, f. 9–16 of t. 5. Aug. 1988. TYPE: *C. W. Wang 87716* (holotype, KUN).

Tree to 16 m high and 40 cm diam. Young twigs dull brown, stout, 5–7 mm diam., villous with long, straight, crisped to undulate, brown to rufous hairs, soon glabrescent; old ones black-brown, fissured and lenticellate, ± hairy to glabrous; terminal buds narrowly ovoid, yellow to brown tomentose. Stipules coriaceous, pubescent with long silky hairs outside, free from the petiole. Leaves coriaceous, rigidulous, dark bright green, at first scattered-pubescent over both surfaces and pilose along the midrib, later glabrescent above, beneath glaucous, appressed-tomentose with same hairs as the young twigs, sooner glabrescent or only pubescent along midrib and nerves, or glabrous everywhere, elliptic to obovate, the margin slightly revolute and bony; 13–21.5(–24) × 4.5–9.5 cm; apex acute to short-acuminate, acumen 3–5 mm long, base cuneate to subrounded; midrib impressed above, prominent beneath; nerves in 12–14 pairs, visible on both sides, reticulation densely netted, prominent on both sides. Petiole pubescent, glabrescent, 2.7–4 cm long. Brachyblasts covered with same indument as young twigs, 3–4 × 0.6–0.8 cm, pedicles absent; spathaceous bracts 3, coriaceous, tomentose outside. Flower golden-yellow, malodorous; tepals 9–12, subsimilar, the outer 3 obovate, glabrous, ca. 5.7 × 3.5 cm, the inner tepals 6–9, narrowly elliptic to spathulate, 4–4.5 × 1.9–2.1 cm; stamens ca. 60 or more, 17–22 mm long, connective appendage triangular, 0.8–1 mm long, filaments 4–6 mm long; gynoecium cylindrical, golden puberulent, ca. 2 cm long, exserted from stamens; gynophore ca. 6 mm long; carpels ca. 63, ovate, 3–4 mm long; styles 1.5–3 mm long, glabrous.

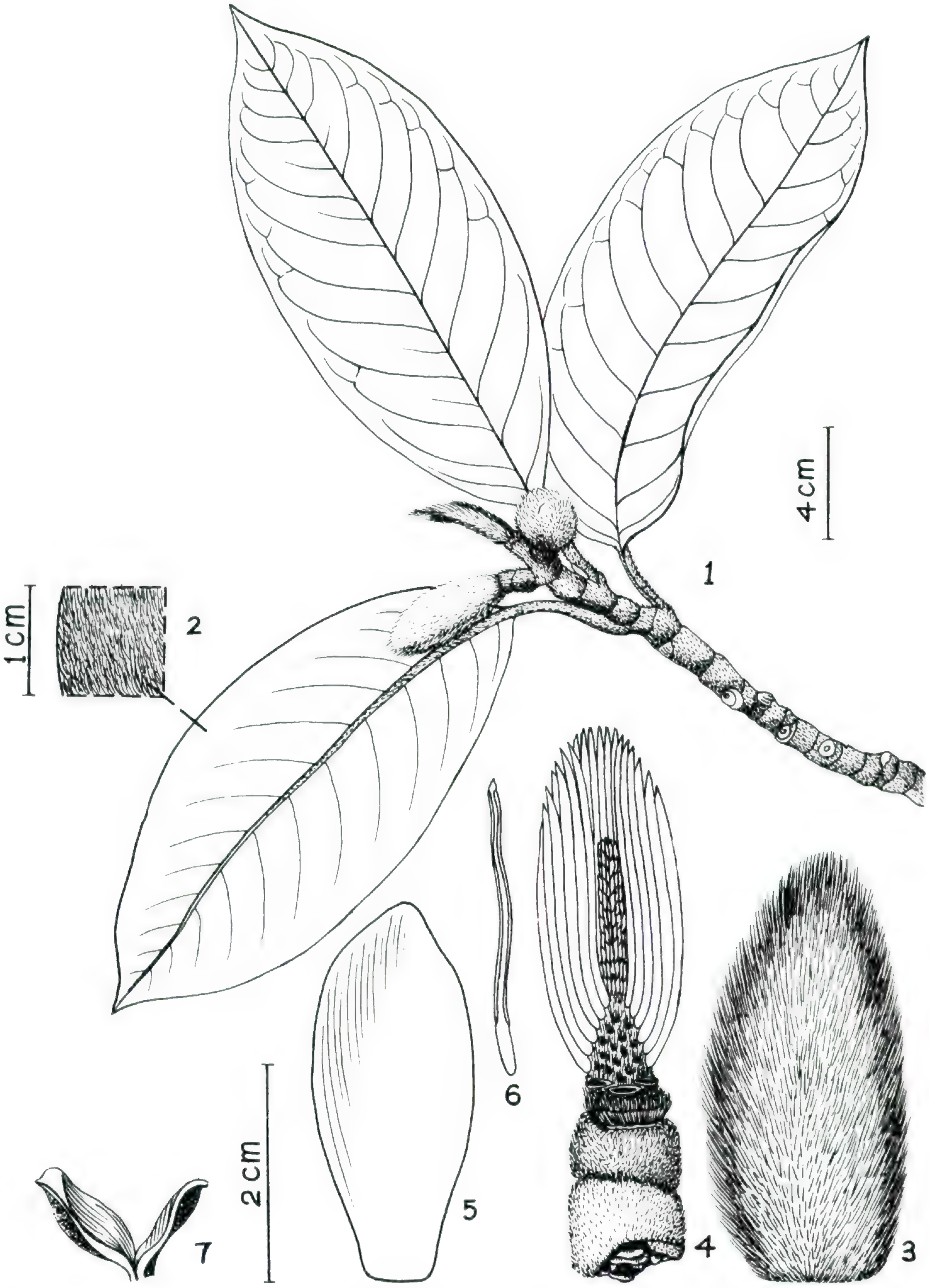


FIGURE 12. *Michelia fulva* H. T. Chang & B. L. Chen.—1. Flowering branch.—2. Underside of leaf.—3. Bract.—4. Deflorated flower with gynoecium and part of androecium.—5. Outer tepal.—6. Stamen.—7. Follicle. Based on *SYS 161751 = Chen Bao Liang G1 86-193*. Drawing by Xie Qing Jian.

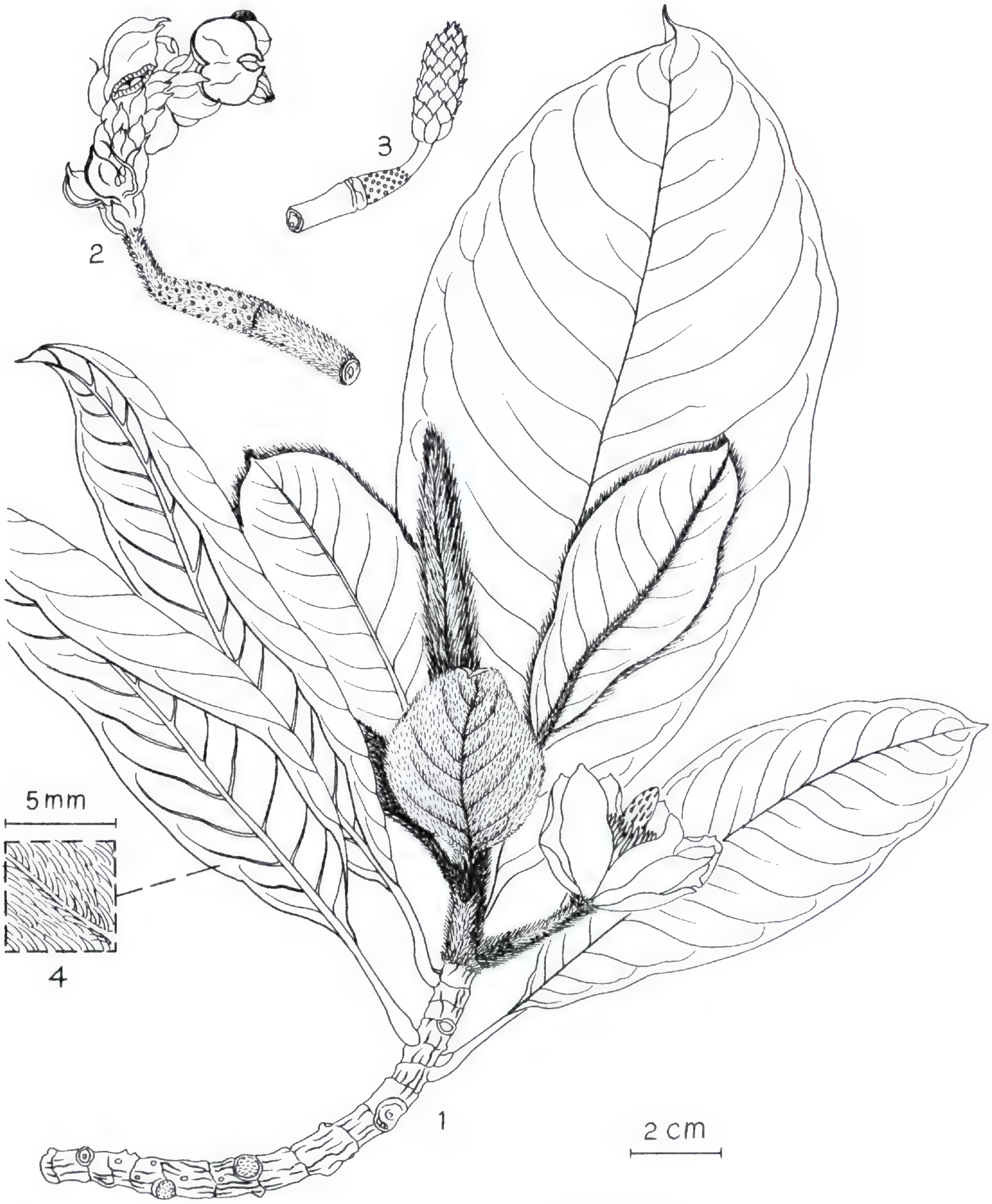


FIGURE 13. *Michelia ingrata* B. L. Chen & S. C. Yang.—1. Flowering branch.—2. Fruit.—3. Deflorated flower showing gynoecium.—4. Undersurface of leaf. Based on *SYS 161515* = *Chen Bao Liang 87 T 019*. Drawing by Xie Qing Jian.

Fruits 6–10 cm long, the fertile carpels sessile, 8.9–14 × 7–10 mm, with 2–5-mm-long beak. Gynophore under fruit 17 × 4 mm. Seeds 2–3 in each carpel.

*Distribution.* CHINA. **Eastern and southern Yunnan**: Goang-nan, *Wang C.W. 87715*; Maguan, *Chen B.L. & C.N. Mai 87 T 19*; Malipo, *Wang C.W. 87033*. Also in Xichou and Guangxi (Longzhou).

*Ecology.* In thickets on limestone. Altitude: 1,600–2,000 m. Flowering March–May.

*Collector's note.* Flowers with putrid smell.

*Note.* This species varies in size of the leaves and length of the peduncles.

14. **Michelia kisopa** Buch.-Ham. ex DC. Syst. Nat. 1: 448. 1817. *Sampacca kisopa* (Buch.-Ham. ex DC.) Kuntze, Revis. Gen. Pl. 1: 6. 1891. TYPE: Nepal, Narain-hetty, 22 Oct. 1802, *Buchanan-Hamilton s.n.* (BM).

*Michelia zila* Buch.-Ham. ex Madden, Trans. Bot. Soc. Edinburgh 5: 127. 1858. TYPE: *Buchanan-Hamilton 1262* (E).

Tree, bark gray; young twigs 1.5–3 mm diam., yellow-brown, purple-brown, to dull brown-black, sparsely minute-puberulent or tomentellous with short, straight to slightly undulate, clear hairs, glabrescent; old twigs brown, gray-brown, to gray-black, longitudinally fissured or wrinkled, sparsely lenticellate. Stipules tomentellous with straight, clear hairs, adnate to the petiole usually up to or beyond half its length, scars 1.4–2 cm long. Leaves thinly coriaceous to coriaceous, bright green, sparsely puberulent, especially on the midrib and toward the base above, paler green, minutely appressed-pubescent with straight, clear hairs, glabrescent beneath, oblong-elliptic, obovate-elliptic, oblong, ovate-oblong to ovate, somewhat unequal; 5.2–16.5(–19) × 2.2–5 cm; apex acuminate to long-acuminate, acumen 7–12(–20) mm long, occasionally acute, base cuneate to rounded; midrib slightly impressed above, nerves in 10–15 pairs, obscure or hardly visible on both sides, reticulation prominent on both sides. Petiole slender, puberulent, glabrescent, 1.6–3.5 cm long. Brachyblast densely tomentose with short, straight to slightly undulate, clear or gray hairs, 4–6 × 3–5 mm, pedicle absent; bracts 3(–4), appressed-tomentose with same hairs as the brachyblast. Flowers not or faintly scented; tepals 9–15, white to yellow, glabrous or puberulent outside toward the base, subsimilar, the outer 3 obovate, obovate-oblong, to spathulate, tapering toward the base, becoming short or long clawed, 3–3.5 × 1–1.3 cm, the inner tepals narrowly obovate-elliptic, 2.2–2.7 × 0.4–0.7 cm; stamens 8–11 mm long, connective appendage usually linguiform or long-triangular, 2–4 mm long, filaments 1–2 mm long; gynoecium cylindric, longer than the androecium, ca. 6–10 × 2 mm; gynophore yellowish tomentellous, ca. 1–4 × 1 mm; carpels ca. 26, ovoid, covered with the same indument as the gynophore; styles short and wide, glabrous; ovules 3–8; scars of perianth and stamens on torus 1–2 × 2.5–3 mm. Fruiting brachyblast ca. 7 × 5 mm. Fruit 3–10 cm long; mature carpels 3–14, nearly globose or ellipsoid, yellow-brown, sessile, beaked apically, ± puberulent, 8–14 × 7–10 mm; scars of perianth and stamens ca. 4 × 4 mm. Gynophore under fruit 1 cm long.

*Distribution.* Southern Kumaon to Sikkim, China. In CHINA: **Xizang**.

*Ecology.* In forests. Altitude: 1,500–2,250 m.

*Uses.* According to Aikin, the wood is used for light construction.

*Note.* See Dandy (1927b).

15. **Michelia lacei** W. W. Smith, Notes Roy. Bot. Gard. Edinburgh 12: 216. 1902. TYPE: *J. H. Lace 5928* (holotype, E; isotype, K).

*Michelia uniflora* Dandy, Kew Bull. 1927: 203. 1927. TYPE: Burma. Mawson, southern Shan States, *N. Manders, 1888* (holotype, K).

*Michelia tignifera* Dandy, J. Bot. 68: 213. 1930. TYPE: *Poilane 12864* (holotype, P; isotype, K).

*Michelia magnifica* Hu, Bull. Fan. Mem. Inst. Biol. (Peiping) 10: 118. 1940. TYPE: *H. T. Tsai 56961* (holotype, PE; isotypes, A, BM).

*Michelia pachycarpa* Law & R. Z. Zhou, Bull. Bot. Res. (China) 7, 1: 85, t. 1987. TYPE: *R. Z. Zhou 25* (IBSC, seen alive).

Tree to 40 m high and 1 m diam.; young twigs stout, 4–6(–10) mm diam., glabrous or at first gray- to yellowish tomentose, later glabrescent, terete, brown-yellow to purple-brown, usually glaucous when dry, conspicuously elliptic lenticellate and with annular scars; old ones longitudinally fissured. Stipules thinly coriaceous, appressed-pubescent with short, straight, yellowish hairs, glabrescent, free from the petiole. Leaves coriaceous, rigidulous, bright green above, pale green beneath, glabrous on both sides, obovate-elliptic to elliptic, 14–28 × 6–10 cm; apex short-acuminate to acute, base cuneate to broadly cuneate, margin somewhat revolute; midrib impressed above, prominent below, nerves in 9–15(–20) pairs, reticulation lax, nerves and reticulation prominent on both sides when dry. Petiole glabrous, wide sulcate above, 2.5–3 cm long, without scars. Brachyblast glabrous to tomentose, 15–25 × 5–7 mm, pedicle absent; bracts 3–4, chartaceous, ± puberulent outside, especially toward the base. Flower fragrant, solitary, sometimes abnormally two-flowered; bud ovoid-cylindric, ca. 4 cm long; tepals 9, white, subsimilar, glabrous, obovate to spathulate, 5.5–7 × 1.5–3 cm; stamens 2–2.5 cm long, connective appendage short-triangular, ca. 1 mm long, filaments 2–3 mm long; gynophore tomentellous, 1–2 cm long, gynoecium 1.7–2 cm long-exserted from stamens; carpels ca. 12, glabrous; styles long and recurved;

ovules ca. 10; scars of perianth and stamens on torus ca. 7 mm long. Fruiting brachyblast 15–25 × 5–10 mm. Fruit 7–10 cm long; ripe carpels 4–6, obovoid, brown to dark brown, lenticellate, ca. 2–4.5 × 2 cm, 5–6 mm thick; gynophore ca. 29 × 6 mm; scars of perianth and stamens ca. 2–2.2 × 0.9 cm.

*Distribution.* China, Vietnam, and Burma. In CHINA. **Southwestern and southeastern Yunnan**: *Chen B.L. 86 S 51, GS 86102, Tsai H.T. 56961.*

*Ecology.* In forests. Altitude: 1,450–1,550 m. Flowering February–March; fruiting September–October.

*Uses.* Wood soft, for planks.

*Collector's note.* Big tree, flowers white, heavily sweet-scented.

Note. The first author has collected material with flowers and fruits from the type tree of *Michelia pachycarpa*. There is no doubt that it is synonymous with *Michelia lacei*.

16. **Michelia macclurei** Dandy, J. Bot. 66: 360. 1928. TYPE: *F. A. McClure 1468* (*in C. C. C. 13292*) (holotype, UC; isotypes, A, K, US).

*Michelia macclurei* var. *sublanea* Dandy, J. Bot. 68: 212. 1930. TYPE: *Tsiang 2609* (holotype, NY; isotypes, A, BM, E, K, P).

Tree to 30 m high and 1 m diam.; bark white-gray; buds, young twigs, stipules, petiole, brachyblasts and bracts outside appressed-tomentellous with short, straight, clear, silver, brown or rufous hairs, glabrescent; young twigs 2–4 mm diam., yellow-brown, blackish to purple-brown; old ones rough, sparsely lenticellate, longitudinally striped. Stipules free from the petiole. Leaves coriaceous, at first somewhat sericeous, later glabrescent above, appressed-tomentose with short to long, straight, rufous (when young) to clear or yellowish (when older), glistening hairs beneath, broadly elliptic to broadly ovate, rhombic-elliptic, or broadly obovate, occasionally narrowly elliptic, 6.5–14 × 4–6.5 cm; apex short-acuminate to acute, base cuneate to broadly cuneate; midrib impressed above, prominent, at first densely brown pubescent with long hairs, soon glabrescent, nerves fine, in 10–15 pairs, conspicuous on both sides; reticulation usually densely netted, prominent on both sides. Petiole sulcate above, 2.5–4 cm long, without stipular scars. Brachyblast 10–13 × 3–4 mm, with 3 bract scars; pedicle 2–5 mm. Tepals 9–12, white, subsimilar, the outer 3 narrowly obovate to spathulate, 3.5–4.5 × 1–1.5 cm, the inner 6–9 smaller and narrower than the outer ones; stamens 9–13 mm long, connective sparsely puberulent, its appendage tonguelike, 1–2 mm long, filaments 1–2 mm long; gynoecium narrowly cylindric, 7–9 mm long, tomentellous, slightly longer than the androecium; gynophore brown tomentellous, 5 mm long; carpels ca. 28 or more. Fruiting brachyblast 10–15 × 4–5 mm, glabrescent. Fruit 3–7 cm long; gynophore 8–10 × 3–4 mm, glabrescent; ripe carpels ellipsoid or subglobose, dull brown, sessile, ± lenticellate, 15–23 × 9–10 mm; scars of perianth and stamens on torus ca. 4–5 × 5 mm. Seeds 1–3, flat-ovoid, 8–10 mm long.

*Distribution.* China and northern Vietnam. In CHINA. **Guangdong**: Fangcheng, *Chun S.H. 4466*; Wuchuan, *Chen S.P. 1131*; Yangchun, *Wang Q 830001.* **Guangxi**: Rongshui, *Long G.R. 830090*; Ronxian, *Liang C.F. 31845*; Yulin, *Lee S.K. 200723.* **Hainan**: Manning, *How F.C. 73194.* Also in Yunnan.

*Ecology.* In mixed forest. Altitude: 500–1,000 m. Flowering March–April; fruiting September–November.

*Uses.* Wood fine-textured, straight-grained and fragrant; commonly used for construction, planks, and furniture; the tree is grown as an ornamental.

*Note.* The indument varies in this species. Therefore, we prefer to reduce *Michelia macclurei* var. *sublanea* to *Michelia macclurei*.

17. **Michelia masticata** Dandy, J. Bot. 67: 222. 1929. TYPE: *Poilane 11253* (holotype, P; isotypes, BM, K).

*Michelia sphaerantha* Law & Y. F. Wu, Acta Bot. Yunnanica 10, 3: 335, t. 1. 1988, nom. illeg., non *Michelia sphaerantha* Z. S. Yue 1987. TYPE: *M. K. Li 2539* (KUN not seen).

See *Michelia sphaerantha* Yue under dubious species.

Tree to 18–25 m high and 80 cm diam.; bark gray-brown, irregularly fissured lengthwise, conspicuously lenticellate; young twigs pubescent or glabrous, slender, bright yellow-green; old ones dark green, with white lenticels; bud cylindric, ca. 13 mm long. Stipules yellowish sericeous or brownish pubescent outside toward the apex, free from the petiole. Leaves coriaceous, dark green, slightly glossy above, pale green beneath, scattered appressed-pubescent with short, straight to slightly undulate, clear to brownish hairs, glabrescent on both sides, broadly elliptic, elliptic-oblong, ovate, or obovate, 12–22(–28) × 5–8(–10) cm; apex short-acuminate, base cuneate to rounded; midrib and nerves impressed above, much prominent below, nerves in 8–13 pairs, reticulation laxly netted, visible on both sides. Petiole appressed-tomentellous, glabrescent, 2–3(–4.5) cm long, without scars.

Brachyblast yellowish sericeous, glabrescent, ca. 10 × 3–4 mm; pedicle absent; bracts 3, covered with same indument as the stipule. Tepals 9–12, white to yellowish white, subsimilar, the outer 3 obovate, narrowly obovate to spathulate, 5–9(–11) × 1–2.5 cm, the inner 6–9 narrower than the outer ones, 3–6(–8) mm long; stamens many, ca. 2 cm long, filament ca. 3 mm, connective appendage ca. 1 mm long; gynoecium cylindric, tomentellous with short, straight, brownish hairs, 3–6(–8) cm long, longer than stamens; gynophore tomentellous, ca. 1 cm long; carpels many, ca. 6 mm long; styles ca. 2.2 mm long; scars of perianth and stamens on torus 6–8 × 5 mm. Fruiting brachyblasts 5–7 cm long. Fruit 10–40(–53) cm long; follicles to 100(–128), dull brown, ovoid to ellipsoid, densely gray-white lenticellate, reddish glandular, apically beaked. Seeds 2–6 in each carpel, red, globose and slightly compressed to irregularly shaped, ca. 10 mm long. Gynophore under fruit ca. 2.5 cm long.

*Distribution.* China, Laos, and Vietnam. In CHINA. **Yunnan**: Wulinag shan, *Tsiang T. 12059*; Menghua, *Yu T.T. 15884*; Nanjiang Xian, *Yue Z.S. 86- 107*; Pingpien, *Mao P.I. 27216*; Chu-hsiun, *Li M.K. 3.*

*Ecology.* In forest. Altitude: 500–2,110 m. Flowering April–May; fruiting October.

*Uses.* Wood hard and dense, useful for all purposes. The tree is grown as an ornamental.

*Note.* We were unable to study the type specimen of *Michelia sphaerantha* C. Y. Wu ex Law & Y. F. Wu. Fortunately, there were some other collections available (including *Mao Ping-i 3621*, *0321*, and *02728*). There is no doubt that *Michelia sphaerantha* C. Y. Wu ex Law & Y. F. Wu (nomen illeg.) belongs to *Michelia masticata*. The only differences are in the degree of indument and the number of carpels. Generally, the Chinese collections have a more dense indument and more carpels. *Michelia sphaerantha*, published by Yue (1987) is based on another type and represents another species.

18. **Michelia maudiae** Dunn, J. Linn. Soc. Bot. 38: 353. 1908. SYNTYPES: *Hongkong Herb. 2449, 2065* (HK, A).

*Michelia chingii* Cheng, Contr. Biol. Lab. Sci. Soc. China, Bot. Ser. 10: 110. 1936. TYPE: *R. C. Ching 2452* (holotype, PE; isotypes, A, E, K).

Tree to 20 m high and 60 cm diam.; bark pale gray or gray-brown; plant entirely glabrous; buds, young twigs, stipules outside, leaves beneath, petiole, brachyblasts, bracts outside, and gynoecium pale green to glaucous when dry; young twigs 2–3 mm diam., dull purple-brown, yellow-black to dull yellow; old ones yellow-gray, black-gray to dull black, lenticellate, longitudinally fissured. Stipules free from the petiole. Leaves coriaceous, dark green, glossy above, broadly elliptic, obovate-elliptic to obovate, 9.5–17.5 × 3–7 cm; apex abruptly short-acuminate, acumen 3–12 mm long, occasionally long-acuminate, to 2 cm long, base cuneate to nearly rounded; midrib flat to ± impressed above; nerves fine, visible on both sides, in 7–12 pairs, reticulation densely netted, prominent on both sides. Petiole 1–3 cm long, without stipular scar. Brachyblast 10–28 × 4–7 mm, pedicle absent; bracts 2–4, sometimes leaflike. Flower solitary, occasionally two, fragrant; tepals 9–12, white, subsimilar, the outer 3 broadly obovate, attenuate toward the base, 5–8 × 2.3–4 cm, the inner tepals 6–9, obovate, elliptic to broadly spathulate, short-clawed at the base, 4.5–5 × 1.8–2.5 cm; stamens 13–17 mm long, connective appendage short to long triangular, 0.5–2 mm long, filaments pale purple, 2–5 × 2 mm; gynoecium subcylindric, longer than the androecium, 10–13 mm long; gynophore 6–12 mm long; carpels many, ovoid, 2–3 mm long; styles 3–3.5 mm long; ovules 6–14 in each carpel; scars of perianth and stamens on torus ca. 4 × 6 mm. Fruiting brachyblast 17–30 × 4–8 mm. Fruits 10–12(–14) cm long; ripe carpels 2–19, obovoid to ovoid, dull brown, lenticellate, short-beaked apically, 1–2.5 × 1–1.7 cm; gynophore 13–30 × 4–5 mm; scars of perianth and stamens 5–6 × 6–7 mm. Seeds subovoid, ca. 1 × 0.5 cm, slightly compressed.

*Distribution.* CHINA. **Fujian**: Yenping, Buong, *Chung H.H. 3667*. **Guangdong**: North river region, *Wang C. 31404*; Ruyuan, *Chen B.L. 80110*; Ying Tak, *Tsang W.T. 3044*; Fan Shiu Shan, *Lau S.K. 2552*. **Guangxi**: Guangyang, *Zhao R.F. 54*; Lingui, *Zhao R.F. 197*; Longshen, *Liu L.F. 5671*; Xingan, *Xing An Exped. 285*. **Guizhou**: Tuhshan, *Tsiang Y. 6933*; Liping Xian, *Yuan J.M. 621*; Lipo county, *Song X.H. 244*. **Hainan**: Jiangyong, *Tam P.C. 63667*. **Jiangxi**: Lungnan distr., *Lau S.K. 4854*. **Zhejiang**: Lungtsuau, *Ho Y.Y. 3200*; Pang Yung, *Ching R.C. 2066*. Also reported from southern Hunan.

*Ecology.* In evergreen broad-leaved forests. Altitude: 500–1,500 m. Flowering February–March; fruiting September–October.

*Uses.* Wood straight-grained and fine-textured, used for furniture and planks.

19. **Michelia mediocris** Dandy, J. Bot. 66: 47. 1928. TYPE: *McClure* in *C. C. C. 8593* (holotype, BM; isotypes, A, E, K, MO).

Tree to 35 m high and 90 cm diam.; bark white-gray; buds rufous or silver appressed-tomentellous; young twigs 2–3 mm diam., dull black-gray to yellow-brown, appressed-tomentellous with short, straight, silver to brown hairs, glabrescent, sparsely lenticellate. Stipules silver appressed-tomentellous, free from the petiole. Leaves thinly coriaceous to coriaceous, bright green, scattered-puberulent with short, straight, clear to brown hairs, especially on midrib and toward the base, glabrescent or glabrous above, ± pale green, at first appressed-tomentellous with short, straight, glistening, yellowish hairs, soon glabrescent beneath, elliptic, broadly elliptic, obovate-elliptic to rhombic-elliptic, 5–10(–13.5) × 3–4(–7) cm; apex acute to acuminate, base attenuate or cuneate to broadly cuneate; midrib prominent, appressed-puberulent with short, straight, brown and yellowish hairs, glabrescent below, nerves rather fine, in 10–15 pairs, obscure to visible on both sides, more prominent beneath than above, reticulation densely netted, conspicuous on both sides when dry. Petiole densely tomentellous with same hairs as young twigs, glabrescent, 1.5–2.5 cm long, without scars. Brachyblast brown or yellow appressed-tomentellous, ca. 6–10 × 3 mm, pedicle ca. 2 mm long; bracts 3–4, silver or brown tomentellous outside. Tepals 9–10, white, subsimilar, obovate, spathulate to obovate-linear, usually attenuate toward the base, clawed at the base, 1.8–3 × 0.4–1.8 cm; stamens 1–1.5 cm long, connective appendage tonguelike, variable in length, 2–4 mm long, filaments 1.5–2 mm long; gynoecium short-cylindric, 6–12 mm long, usually longer than the androecium, occasionally equal to the latter; gynophore gray to brown tomentellous, 3–5 mm long; carpels 13–18, tomentellous with same hairs as gynoecium; ovules 4–6; scars of perianth and stamens on torus ca. 3 × 3 mm. Fruiting brachyblast ca. 1 × 0.4 cm, tomentellous. Fruit 2–3.5(–5) cm long; carpels glabrescent, obovoid to ellipsoid, slightly compressed, sessile, ca. 2 × 1.2 cm; gynophore under fruit 5–8 mm long. Seeds 5–8 mm long.

*Distribution.* China, Cambodia, and Vietnam. In CHINA. **Guangdong**: Dinghushan, *Shi G.L. 14241*; Fachou distr., *McClure F.A. 582*. **Guangzhou**: *Wang X.W. 5690*; Kochow, *Pasheng 2*; Yingde Xian, *Liang H.Y. 61546*. **Guangxi**: Dafongshan, *Chang C.C. 11316*; Zhaoping Xian, *Li Y.K. 402692*. **Hainan**: Bawangling, *Zheng P. 13465*; Chim Fung Mt., *Lau S.K. 5245*; Five Finger Mts., *McClure F.A. CCC 8593*; Hung Mo Tung, *Sing I.Y.* (herb.nr 18350) *817*; Tianchi, *Wang C. 2888*.

*Ecology.* In forest. Altitude: 400–1,300 m. Flowering December–January; fruiting June–July.

*Uses.* Sapwood yellow-brown, heartwood brown-yellow; wood straight-grained, fine-textured, light, soft, and durable; commonly used for furniture, millwork, veneer, plywood, musical instruments, and also for bridges and ships.

*Collector's notes.* On sandy soil; flowers fragrant.

*Note.* G. W. Groff, Ding & Groff (1923) and Merrill (1927a) misidentified this species as *Michelia maudiae* (auct. non Dunn, 1908).

20. **Michelia microtricha** Hand.-Mazz., Akad. Wiss. Wien 58, 18: 81. 1921. TYPE: *Ten 339* (holotype, C; isotypes, K, V). Figure 14.

Tree to 3–20 m high. Young twigs 2–3 mm diam., dull yellow-brown or black-brown, appressed-tomentellous with minute, straight, brown to gray hairs, glabrescent; old ones dull brown, ± pubescent, lenticellate; buds narrowly ovoid, 1.2 cm long. Stipules minutely gray or dark brown tomentellous outside, stipular scars ca. 1.5 cm long. Leaves coriaceous, dark green, glossy, appressed-puberulous with straight, clear to gray hairs, especially on the midrib and toward the base above, glabrescent, appressed-tomentellous with short, straight, yellowish to brown hairs beneath, elliptic to narrowly obovate, 8–16 × 3–5 cm; apex acute to short-acuminate, base cuneate; midrib impressed above, conspicuous below, nerves fine, visible on both sides, in 8–14 pairs, reticulation densely netted, obscure on both sides. Petiole tomentellous, glabrescent, narrowly sulcate above, 2.5–3 cm long. Brachyblast densely tomentose, 7–10 × 3.5–4 mm, pedicle ca. 3 × 4 mm; bracts 3, broadly ovate, cupreous sericeous outside, 3.5–3.9 cm long. Flower bud long-ovoid; tepals 12, white, fleshy, the outer 3 obovate to spathulate, abruptly constricted near the middle or tapering gradually toward the base, finally becoming long clawed, 3.2–3.7 × 1.4–1.5 cm, the inner tepals 6, spathulate, ca. 3–3.7 × 1.2 cm, the 3 innermost ones obovate-linear, ca. 2.5 × 0.8 cm; stamens numerous, 10–11 mm long, connective appendage short triangular, 1–2.5 mm long; filaments 1–2.5 mm long; gynoecium subcylindric, 6–11 mm long; gynophore minutely puberulent with clear or brownish hairs, ca. 4 mm long; carpels ca. 25–40, ellipsoid, covered with the same indument as gynophore; styles glabrous, erect, 1–1.5 mm long; ovules 6–8; scars of perianth and stamens on torus ca. 2 mm long. Fruit not seen.

*Distribution.* CHINA. **Yunnan**: Lungtji, Peyentjing, Dali, *Teng, S.M. 339*; Jinping, *Wu S.K. 3867*.

FIGURE 14. *Michelia microtricha* Hand.-Mazz. — 1. Flowering branch. — 2. Deflorated flower. — 3. Fragment of leaf underside. Based on *Simeon Ten 339* (WU). Drawing by Joop Wessendorp, Rijksherbarium, Leiden.

*Ecology.* In forest.

*Note.* *Michelia microtricha* is relatively rare and is closely related to *Michelia floribunda*. It differs from the latter chiefly by the indument with minute hairs and by the longer brachyblasts.

21. **Michelia shiluensis** Chun & Y. Wu.

See under dubious species.

22. **Michelia velutina** DC., Prodr. 1: 79. Jan. 1824. TYPE: Nepal: *Wallich s.n.* (K).

*Michelia lanuginosa* Wall., Tent. Fl. Nepal., 1: 8, t. 5. June 1824. *Sampacca lanuginosa* (Wall.) Kuntze, Revis. Gen. Pl. 1: 6. 1891. TYPE: *Wallich 6493* (holotype, K; isotypes, A, BM).

*Michelia lanceolata* E. H. Wilson, J. Arnold Arbor. 7: 237. 1926. TYPE: *J. F. Rock 6919* (holotype, A; isotypes, E, NY, UC).

Tree to 15–20 m high by 90 cm diam.; bark dull brown; indument yellowish to brown, sometimes glossy; young twigs 2–3 mm diam., brown to purple-black, pubescent with short, appressed or spreading, undulate to curly hairs, glabrescent; old ones ± hairy. Stipules densely pubescent with long, straight or undulate hairs outside, adnate to the petiole, stipular scars 3–5(–11) mm long. Leaves chartaceous to thinly coriaceous, dark green, glabrous or scattered-pubescent with slender, undulate hairs, especially dense on the midrib above, paler green, densely appressed-pubescent with long, undulate, clear or brown hairs, seemingly velvet, finally glabrescent below, narrowly elliptic, sometimes elliptic to broadly elliptic or ovate-elliptic, (6.2–)11–24(–29.5) × (2.5–)3.5–6.5(–8.5) cm; apex acute to short- or long-acuminate, acumen 1–1.7 cm long, occasionally obtuse, base cuneate to rounded; midrib impressed above, prominent below, nerves fine, slightly impressed, obscure above, visible beneath, in 11–23(–28) pairs, reticulation densely netted, faint on both sides. Petiole densely pubescent, glabrescent, somewhat dilatate toward the base, 0.9–1.4(–2.3) cm long. Brachyblast densely pubescent with short, undulate to curly, yellowish or brown hairs, 4–17 × 4–5 mm, pedicle 0–2 mm long; bracts 3, pubescent with same hairs as stipules outside. Flower bud long-ovoid, ca. 2.7 cm long; flower very fragrant; tepals 10–12(–13), white to yellowish, subsimilar, spathulate to elliptic-linear, basally long-clawed, the outer 4–6 glabrous to puberulent outside at the base, 2.2–5.5 × 0.7–0.8 cm; stamens 9–12 mm long, connective appendage triangular, 1–2 mm long, filaments ca. 2 mm long; gynoecium ovoid-oblong to narrowly ovoid, longer than the androecium, 9–15 × 3–6 mm; gynophore densely pubescent, 6–7 × 2–3 mm; carpels ca. 35, subglobose, densely pubescent; styles erect, glabrous, ca. 1 mm long; ovules 3–6 in each carpel; scars of perianth and stamens on torus 3–5 × 4–5 mm. Fruiting brachyblast ± pubescent, ca. 1–1.7 × 0.5 cm. Fruit 3.5–13 cm long; ripe carpels ovoid to ellipsoid, dull brown, densely lenticellate outside, stipitate, 7–25 × 10–17 mm; gynophore 17–20 × 4–4.5 mm; scars of perianth and stamens ca. 5 × 5 mm. Seeds subcordate to subglobose, 7–10 × 6–8 mm.

*Distribution.* CHINA. **Xizang**: Putsang River, Rong To valley, Zayul, *Kingdon Ward F. 10980.* **Yunnan**: W of Talifu, Mekong watershed, *Rock J.F. 6919*; Che li Hsien, *Wang C.W. 78441*; Chu hsian, *Li M.K. 59.*

*Ecology.* In mixed forests. Altitude: 1,500–2,300 m. Flowering May–June; fruiting August–September.

*Uses.* Wood usually grayish white and soft, not useful.

23. **Michelia wilsonii** Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 45, t. 7A. 1905. TYPE: *Wilson 3136* (holotype, P; isotypes, A, BM, K).

*Michelia sinensis* Hemsl. & E. H. Wilson, Kew Bull. 1906: 149. 1906. TYPE: *Wilson* (*Veitch Exped.*) *3136* (holotype, K; isotypes, A, BM, P).

*Michelia szechuanica* Dandy, Notes Roy. Bot. Gard. Edinburgh 16: 131. 1928. TYPE: *Wilson 4598* (holotype, K; isotype, A).

Tree to 20 m high; indument appressed to spreading; young twigs 1–3 mm diam., yellow or black-brown, glabrous to tomentose; old ones brown to purple-brown, lenticellate. Stipules densely pubescent with short, straight to undulate, yellowish to brown hairs, adnate to base of the petiole, scars 1–5 mm long. Leaves thinly coriaceous, dark green, glossy, pubescent especially on the midrib, later glabrescent above, glaucous, at first densely pubescent or tomentellous with minute, straight or undulate, yellowish to brown hairs, finally glabrescent beneath, obovate, obovate-elliptic, narrowly obovate-elliptic, rarely broadly elliptic, somewhat unequal, 11.5–14(–18) × 4–6 cm; apex short-acuminate, acumen 4–10 mm long, occasionally acute, base attenuate to cuneate or broadly cuneate; midrib slightly impressed above, nerves obscure above, visible below, in 8–13 pairs, reticulation densely netted, faint on both sides when dry. Petiole pubescent, glabrescent, 1.2–1.5 cm long. Brachyblast pubescent with short, undulate hairs, 7–10 × 3–8 mm, pedicle absent; bracts 3(–4),

pubescent outside. Flower bud ovoid to ellipsoid, ca. 13 mm long; flower fragrant; tepals 9–12, yellowish white, subsimilar, obovate to spathulate, 2–3 × 0.6–0.8 cm; stamens 10–12 mm long, connective appendage very short-triangular, ca. 0.5 mm long, filaments 2–2.5 mm long; gynoecium cylindric, longer than the androecium, ca. 14 mm long; gynophore tomentellous, 2–3 mm long; carpels many, brown or silver tomentellous; ovules 6 or more; scars of perianth and stamens on torus 2–2.5 × 3–3.5 mm. Fruiting brachyblast ± pubescent, ca. 11 × 8 mm. Fruit 13.5–15.5 cm long; ripe carpels subglobose, ovoid to ellipsoid, purple-brown, lenticellate outside, sessile to short-stipitate, apex curved-beaked, 10–20 × 15 mm; gynophore 2–2.2 cm × 0.4–0.5 mm.

*Distribution.* CHINA. **Guizhou**: Chishui Xian, *Dang C.Z. 1656*. **Hubei–Sichuan**: Metaseqoia area, *Hwa C.T. 502*. **Jiangxi**: *Li Z.Z. 8220423*. **Sichuan**: Nanchuan, *Yang G.H. 54716*; Mabian, *Chang Q.L. 12055*; Kai Hsien, *Wilson E.H. 4598*; Mt. Omei, *4720*.

*Ecology.* In forests. Altitude: 1,000–1,500 m. Flowering March–May; fruiting August–September.

*Collector's note.* In forests on slope or in temple gardens.

*Note.* *Michelia sinensis*, like *Michelia szechuanica*, is not different from *Michelia wilsonii*. The type specimen of *Michelia szechuanica* possesses appressed hairs, whereas that of *Michelia wilsonii* has spreading hairs. Unfortunately, we did not have much material to study, but in some collections examined we observed an intermediate indument.

24. **Michelia ×alba** DC., Syst. Nat. 1: 449. 1817. TYPE: This species is based on *Sampaca domestica* IV *alba* Rumph., Herb. Amboin. 2: 200. 1741.

*Michelia longifolia* Blume, Verh. Batav. Genootsch. Kunsten 9: 155. 1823. *Sampaca longifolia* O. Kuntze, Rev. Gen. Pl. 1: 6. 1891. TYPE: *Blume s.n.* (L, sheet no. 908.126-1242; isotype, K).

*Michelia longifolia* var. *racemosa* Blume, Fl. Javae Magnoliaceae: 13, t. 3. 1829. TYPE: *Blume s.n.* (L).

Tree to 30 m high, bark gray; young twigs and buds densely grayish appressed-pubescent or puberulent, soon glabrescent. Stipules covered with same indument as the young twigs, adnate to the base of the petiole, stipular scars never over halfway the length of the petiole. Leaves thinly coriaceous, glabrous above, sparsely pubescent below, elliptic to obovate-elliptic, 10–35 × 4–11 cm; apex acuminate, acumen 7–30 mm long, base cuneate. Petiole sparsely appressed-puberulent to glabrous, 1.5–5 cm long. Brachyblasts with 2–3 evenly distributed scars, densely grayish pubescent. Flowers often many, nicely scented, white; tepals 10–12, subequal, lanceolate, 3–5.5 × 0.3–0.5 cm; stamens 8–10 mm long, connective appendage tonguelike, 1–1.5 mm long, filaments 1–1.5 mm long; gynoecium minutely hairy, exserted from the androecium, 8–13 mm long; carpels ca. 10; gynophore grayish puberulent, 2–4 mm long. Fruits usually with a few ripening carpels but most carpels abortive, 10–13 cm long; ripe carpels ovoid to ellipsoid, 1.2–1.8 cm × 8–12 mm, ± hairy, beaked at the apex; gynophore 18–24 mm long; scars of perianth and stamens ca. 16 × 6 mm. Fruiting peduncle pubescent, glabrescent, 1.7–3.2 × 0.5 cm.

*Distribution.* Widely cultivated in southern Fujian, Guangdong, Hainan, Guangxi, and Yunnan, as well as in other tropical and subtropical countries.

*Ecology.* Flowering April–September.

*Uses.* Flower and root used for medicinal purposes, flowers and leaves for volatile oil; the tree is grown as an ornamental.

*Note.* Ridley (1913) and Merrill (1921a p.p.) dealt with this species under *Michelia champaca* (auct. non Linnaeus, 1753). It is probably a hybrid of *Michelia champaca* L. and *Michelia montana* Blume.

**2. Michelia** section **Anisochlamys** Dandy in Praglowski, World Pollen Spore F. 3: 5. 1974. TYPE SPECIES: *Michelia mannii* King.

Stipules free from the petiole, the latter at least 10 mm long. Bracts 3. Tepals 9, 3-merous, very dissimilar, those of the outer whorl much shorter and narrower than those of the inner whorls. Fruits apocarpous.

25. **Michelia hypolampra** Dandy, J. Bot. 66: 32. 1928. TYPE: *Fleury* in *Chevalier 30158* (holotype, P; isotype, K).

*Talauma gioii* A. Chev., Bull. Econ. 132: 790. 1918. TYPE: *Service forestier 38204* (holotype, P).

*Michelia hedyosperma* Law, Bull. Bot. Res. (China) 5, 3: 123, t. 3. 1985. TYPE: *L. C. Chia & S. L. Feng 605* (IBSC not seen).

Tree to 21 m high and 60 cm diam.; buds, stipules outside, young petiole, brachyblast, bracts outside, carpels and gynophore densely covered with minute, straight or slightly undulate, clear to silver, appressed hairs; young twigs slender, 1–2 mm diam., dull brown or black-gray, glabrous; old

ones dull gray, longitudinally wrinkled. Stipules free from the petiole. Leaves thinly coriaceous, glabrous on both sides, or sparsely puberulent, on both the midrib and the margin near the base above, bright green, glossy, broadly elliptic, elliptic to obovate-elliptic, 6–13 × 3–6 cm; apex acuminate, acumen 4–10 mm long, occasionally acute, base cuneate, ± attenuate along the petiole; midrib slightly prominent above, prominent beneath, nerves fine, in 8–16 pairs, reticulation fine and dense, nerves and reticulation prominent on both sides. Petiole wide sulcate above, 1–2 cm long, without scars. Brachyblast rather short, 3–4 × 1.5–2 mm, pedicle absent to very short; bracts 3. Flower buds oblong to ellipsoid, ca. 1 cm long; tepals 9, dissimilar, the outer 3 membranous, linear, ca. 15 × 1 mm, the inner tepals 6, narrowly elliptic, 15–20 × 0.4–6 mm; stamens ca. 25, 8–9 mm long, connective appendage triangular, 1–1.5 mm long, anthers ca. 5 mm long; gynoecium ovoid, 1–2 cm long, exserted from stamens; gynophore 4–6 × 1 mm; carpels 4–10, free from each other, narrowly elliptic, 6–7 mm long; styles ca. 2 mm long, recurved; ovules 6–8; scars of perianth and stamens on torus ca. 2–3 × 2 mm. Fruiting brachyblast 5–20 × 2–5 mm, ± puberulent. Fruit 3.5–4 cm long; ripe carpels ovoid to obovoid-ellipsoid, gray brownish to brownish, densely lenticellate, with a stipe 3–8 mm long at the base, beaked at the apex, 2–4.5 × 1–2.5 cm; gynophore 2–3 × 0.2–0.5 cm; scars of perianth and stamens ca. 4 × 5 mm. Seeds irregularly shaped, 1–4 in each ripe carpel, 9–10 × 6–8 mm.

*Distribution.* CHINA. **Southwestern Guangxi**: Longzhou, *Huang D.Z. 3883*; Ningming, *Liang J.Y. 100316*; Nonggan, *Chang H.T. 6825.* **Hainan**: Bawangling, *Zheng P. 13419.* **Southern Yunnan**: Xishuang Banna, *Li Y.H. 4262.*

*Ecology.* In broad-leaved forest. Altitude: 300–800 m. Flowering March–April; fruiting September–October.

*Uses.* Wood straight-grained and fine-textured, suitable for furniture, construction work, and plywood; crown elegant and flower scented, thus the tree is grown for timber as well as an ornamental.

*Note.* There was no type specimen of *Michelia hedyosperma* available for study. Based on Law's description and figure, there is no doubt, however, that *Michelia hedyosperma* is conspecific with *Michelia hypolampra.*

This species differs strikingly from other species in *Michelia* by rather small flowers with linear outer tepals and few carpels.

**3. Michelia** section **Dichlamys** Dandy in Praglowski, World Pollen Spore Fl. 3: 5. 1974. TYPE SPECIES: *Michelia balansae* (A. DC.) Dandy.

Stipules free from the petiole. Bracts 3–6. Tepals 6 (or occasionally 4), 2-merous, subsimilar. Fruits apocarpous.

KEY TO THE SPECIES OF *MICHELIA*

SECTION *DICHLAMYS*

1. Leaves glabrous. ..... 2
1. Leaves hairy beneath at least when young. ..... 3
2(1). Twigs pubescent, stipules pubescent, leaf base broadly cuneate or attenuate-cuneate, apex short-acuminate or acute, reticulation densely netted; scars of perianth and stamens along torus under fruit 6–8 mm long. ..... 30. *Michelia martinii*
2. Twigs tomentellous, stipules glabrous, puberulous, or tomentellous, leaf base cuneate or rounded, apex acuminate, reticulation laxly netted; scars of perianth and stamens along torus under fruit 4–5 mm long. ..... 29. *Michelia chapensis*
3(1). Gynophore 3–4 mm long, treelet to 4 m high, leaves 1.5–2.5 cm broad, apex rounded; outer tepals spathulate, gynoecium ellipsoid. ..... 26. *Michelia angustioblonga*
3. Gynophore 5–10 mm long, tree to 15–18 m high, leaves 2.8–16.5 cm broad, apex short-acuminate, acuminate, or acute; outer tepals obovate, oblong, or elliptic, gynoecium ovoid or cylindric. ..... 4
4(3) Pedicle present, twigs tomentellous, stipules glabrous or tomentellous, apex acuminate or acute, reticulation rather obscure, petiole not dilated at base; gynoecium cylindric. ..... 29. *Michelia leveilleana*
4. Pedicle absent, twigs pubescent, stipules pubescent, apex short-acuminate, reticulation distinct, petiole dilated at base; gynoecium ovoid. ..... 27. *Michelia balansae*

**26. Michelia angustioblonga** Law, Bull. Bot. Res. (China) 6(2): 97. 1986. TYPE: *Z. R. Xu L12163* (holotype, IBSC; isotype, SYS). Figure 15.

Treelet to 4 m high; indument appressed, glistening; buds densely brown villous; twigs nearly black-brown. Stipules free from the petiole. Leaves coriaceous, dark green, glabrous above, pale green, brown villous beneath, narrowly oblong, 6.5–10 × 1.5–2.5 cm; apex obtuse, base cuneate to broadly cuneate; midrib impressed above; nerves anastomosing, obscure; reticulation densely netted. Petiole 1–1.5 cm long. Brachyblasts sparsely brown pilose. Flowers white, tepals 6, subsimilar, narrowly obovate to spathulate, the outer three 18–20 × 4–5 mm, the inner three 14–16 mm long; stamens 11–15 mm long, anthers 6–10 mm long, connec-

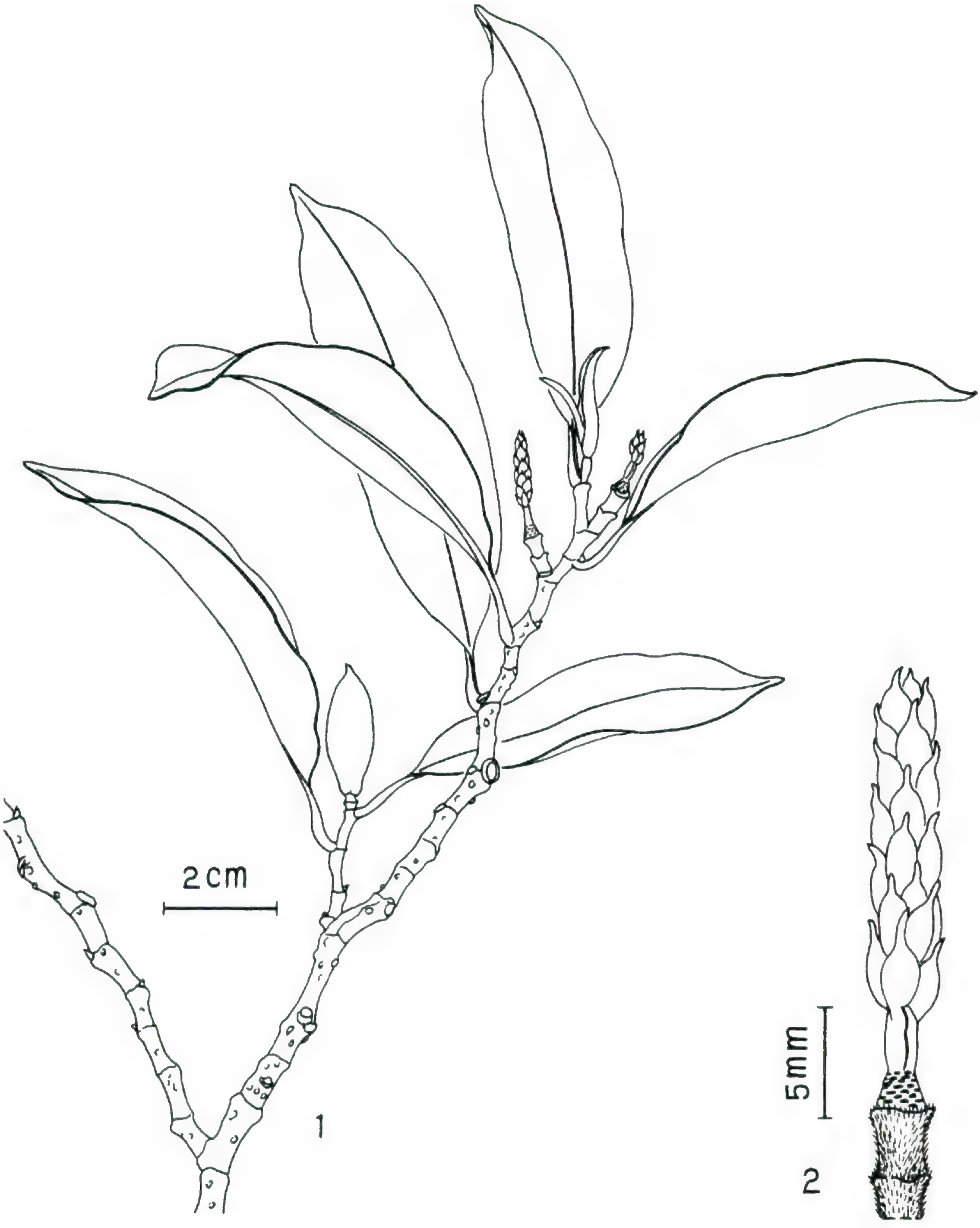


FIGURE 15. *Michelia angustioblonga* Law.—1. Flowering branch.—2. Deflorated flower with gynoecium. Based on *SYS 164643 = Xu Zhao Ran L 12163*. Drawing by Xie Qing Jian.

tive appendage triangular, ca. 1 mm long, filaments 2–3 mm long; gynoecium narrowly ellipsoid, entirely hidden by the androecium, 1–1.5 cm long; gynophore 3–4 mm long; carpels brown pubescent; scars of perianth and stamens on torus ca. 3 × 3 mm. Fruits not known.

*Distribution.* CHINA. **Guizhou**: Libo, *Z. R. Xu L1263*.

*Ecology.* In forest.

27. **Michelia balansae** (A. DC.) Dandy, Kew Bull. 1927: 263. 1927. *Magnolia balansae*

A. DC., Bull. Herb. Boissier 4: 294. 1904. *Michelia baviensis* Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 44, t. 5B. 1905. TYPE: *Balansa 3886* (holotype, P; isotype, L).

*Michelia tonkinensis* A. Chev. ex Gagnep. in Humbert, Fl. Indo-Chine Suppl.: 44. 1938. TYPE: No specimen has been preserved in Chevalier's herbarium.

*Michelia balansae* var. *appressipubescens* Law, Bull. Bot. Res. (China) 5, 3: 124. 1985. TYPE: *S. P. Kuo 52279* (holotype, IBSC; isotypes, A, BM, K, NY).

*Michelia balansae* var. *brevipes* B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 112. 1988. TYPE: *B. L. Chen & C. N. Mai 87TO34* (SYS).

Tree to 18 m high and 60 cm diam.; bark smooth, gray or gray-brown; indument with long, straight to slightly undulate, spreading to appressed, dark brown or brownish to yellowish hairs; young twigs 2–5 mm diam., densely pubescent, subterete, dull brown; old ones glabrescent, sparsely lenticellate. Stipules densely pubescent, free from the petiole. Leaves thinly coriaceous, at first scattered-pubescent, especially on the midrib, later glabrescent above, pubescent, glabrescent beneath, elliptic to broadly elliptic or obovate-elliptic to narrowly obovate-oblong, 8–21.5(–28) × 4.5–10(–16.5) cm; apex short-acuminate to sometimes acute, acumen 3–5 mm long, base cuneate to obtuse; midrib impressed above, prominent below; nerves visible on both sides, more prominent below than above, in 12–14(–19) pairs; reticulation laxly netted, prominent when dried. Petiole pubescent, glabrescent, conspicuously dilatate toward the base, 1.9–4.5 cm long, without scars. Brachyblast densely pubescent, 1.2–3.7 cm long, ca. 3 mm wide, pedicle absent; bracts 3, densely pubescent outside. Flower fragrant; tepals 6, subsimilar, the outer 3 ± appressed-tomentellous outside, white or greenish white to yellow, narrowly obovate-oblong, 3.5–3.7 × 1.3–1.5 cm, the inner tepals 3, spathulate, narrower and smaller than the outer ones; stamens 7.5–15 mm long, connective appendage short-triangular, ca. 0.5 mm long, filaments 0.5–2 mm long; gynoecium ovoid, 1–1.4 cm long; gynophore tawny tomentose, 5–7 mm long; carpels ovoid, tomentose; styles glabrous; ovules ca. 6–11; scars of perianth and stamens on the torus 3–4 mm long. Fruiting brachyblast 1.2–7 × 0.3–1.1 cm, glabrescent. Fruit 4–12 cm long; ripe carpels ovoid to ovoid-ellipsoid, dull dark brown, glabrescent, usually densely small lenticellate, 2–6.5 × 1.3–1.8 cm, ligneous, apically with a stout beak of 3–5 mm long; scars of perianth and stamens 5–10 × 5–14 mm. Seeds ellipsoid, ovoid, subcordate to irregularly shaped, 1–3 in each carpel, 10–15 × 8–12 mm.

*Distribution.* China and Vietnam. In CHINA. **Southern Fujian**: Guangdong, Kung Ping Shan, *Tsang W.T. 26866*; Yaichow, *How F.C. & N.K. Chun 70147*. **Guangxi**: Fang Cheng distr., *Tsang W.T. 26868*; Jingxi, *Ko S.P. 55702*; Shiwandashan, *Tso C.L. 23510*; Yangshou, *Qin H.F. 53*; Nanning, *Liang C.F. 34214*. **Hainan**: Boting, *Lau S.K. 27946*; Jianfong, *Chang H.T. 6081*; Lehui, *How F.C. 73242*; Lin Fa Shan, Lam Ko Distr., *Tsang W.T. (LU 15822) 323*; Lingshui, *Tso C.L. 43749*. **Yunnan**: Funing, *Wang C.W. 89653*; Malipo, *86545, Feng K.M. 13599*; Ping pien hsien, *Tsai H.T. 61621*.

*Ecology.* In evergreen broad-leaved forest, in shaded and mixed forests, along stream side, on moist sandy soil. Altitude: 350–1,000 m. Flowering April–June; fruiting September.

*Uses.* Heartwood brown-yellow, sapwood yellowish brown; wood straight-grained, fine- and even-textured, slightly heavy and durable, commonly used for furniture, plywood, and constructions.

*Collector's note.* Trees dark gray covered with purple hairs, flowers white, greenish white, yellowish or red, fragrant.

*Note.* *Michelia balansae* is a distinct species. Variations in the indument, size of the leaves, and length of the brachyblasts are very noticeable. The indument of *Michelia balansae* var. *appressipubescens* is appressed-pubescent on the leaves beneath and the petioles. However, a continuous variation of the indument can be seen within the species; for example, an indument with short and long, straight and slightly undulate, appressed, spreading hairs is found in the collections of *N. K. Chun & C. L. Tso 43749*; the indument is short, straight, and appressed in *S. P. Ko 52279* and *F. C. How 73480*. The brachyblasts are rather short in the collections of *Michelia balansae* var. *brevipes* collected in southeastern Yunnan, but intermediate forms are found throughout the area of distribution.

28. **Michelia chapensis** Dandy, J. Bot. 67: 223. 1929. TYPE: *Pételot 3379* (holotype, UC; isotypes, BM, NY). Figure 16.

*Michelia constricta* Dandy, J. Bot. 67: 223. 1929. TYPE: *Chevalier 30744* (holotype, P).

*Michelia tsoi* Dandy, J. Bot. 68: 213. 1930. TYPE: *Tso 21033* (NY).

*Michelia glaberrima* Chang, Acta. Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 54. 1961. TYPE: *H. T. Tsang 22753* (holotype, SYS; isotype, A).

*Michelia microcarpa* B. L. Chen & S. C. Yang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 3: 96. 1988. TYPE: *B. L. Chen & C. N. Mai 87T011* (holotype, SYS).

*Michelia chartacea* B. L. Chen & S. C. Yang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 3: 97. 1988. TYPE: *B. L. Chen & S. C. Yang 87F186* (holotype, SYS).

FIGURE 16. *Michelia chapensis* Dandy.—1. Fruiting branch.—2. Upper side of leaf with venation.—3. Flower bud. Based on *SYS 161739 = Chen Bao Liang 87 T 033*. Drawing by Xie Qing Jian.

*Mchelia brachyandra* B. L. Chen & S. C. Yang, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 3: 98. 1988. TYPE: *B. L. Chen & S. C. Yang 87F202* (holotype, SYS).

*Michelia nitida* B. L. Chen, Acta Sci. Nat. Univ. Sunyatseni (Guangzhou) 1: 111. 1988. TYPE: *B. L. Chen & C. N. Mai 87TO33* (holotype, SYS).

Tree to 15–30 m high and 1 m diam.; bark gray-brown, smooth; young twigs brown to dull dark brown, 2–3 mm diam., smooth, glabrous or at first densely appressed-tomentellous with short, straight, brownish hairs, later glabrescent, with suborbiculate, white lenticels; old ones gray to brownish, fissured longitudinally; terminal buds narrowly ovoid, ca. 1 cm long. Stipules glabrous to puberulent or tomentellous outside, free from the petiole. Leaves coriaceous or thinly coriaceous, glabrous, pale brown when dry on both surfaces, obovate or obovate-oblong, occasionally elliptic-oblong or elliptic, 5.5–16 × 2.6–6.5 cm; apex acuminate to subacuminate, base cuneate to obtuse or rounded, slightly unequal; midrib prominent below, impressed above; nerves visible on both sides, in 9–12 pairs, reticulation coarse. Petiole slender, longitudinally grooved above, glabrous or ± minutely appressed-pubescent, 1.5–2.5 cm long, without scars. Brachyblasts tomentellous or puberulent, 3–11 mm long, 2–4 mm wide at top, pedicles 0–3 mm long; bracts 3–4, tomentellous or puberulent outside. Tepals 6, yellow to pale yellowish, glabrous or puberulent outside at the very base, subsimilar, the outer 3 (narrowly) obovate-oblong, convex outside, 3–3.5 cm long, the inner tepals slightly narrower; stamens 14–22 mm long, connective appendage triangular, 1–1.5 mm long, filaments glabrous, ca. 4 mm long; gynoecium glabrous but sometimes sparsely hairy, narrowly cylindric, entirely hidden by the androecium or slightly exceeding it, 11–15 mm long; gynophore 5–7 mm long, silver gray tomentellous with appressed hairs; carpels many, with same indument as gynophore. Fruiting brachyblasts 6–12 × 3–5 mm. Fruits cylindric, 3–10 cm long; ripe carpels 1–14 or more, oblong to ovoid, 6–15 × 8–10 mm, apically short-beaked, sparsely beset with inconspicuous lenticels; gynophore ± pubescent, 8–12 × 3–4 mm; scars of perianth and stamens on torus 4–5 mm long. Seeds obovoid to oblong-ovoid, ca. 10 × 6 mm.

*Distribution.* China and northern Vietnam. In CHINA: **Guangdong**: Kook Kaing, *Ko S.P. 50777*; Kwai Shan, *Tsang W.T. 28559*; Lok Chong, *Tso C.L. 21033*; Nanxiong Xian, *Liu Y.Z. 1*. **Guangxi**: Damiaoshan, *Chen T.C. 707*; Debao, *Chang C.C. 13670*; Gongdeng, *He J.D. 5040*; Guan Xian, *Chen Z.Z. 52375*; He Xian, *Li Y.K. 401573*. **Guizhou**: Congjiang, *Yuan J.M. 692*; Liping Xiang, *Yuan J.M. 373*. **Hunan**: Zixing Xian, *Liang P.H. 86163*. **Jiangxi**: Chongyi, *Nie M.X. 8831*; Jingan, *Gongda 1547*; Shangsa, *Yang X.X. 831164*. **Yunnan**: Xichou, *Wu C.A. 62012*; Marlipo, *Feng K.M. 13973*.

*Ecology.* In evergreen broad-leaved forests. Altitude: 500–1,650 m. Flowering March–April; fruiting August–October.

*Uses.* Wood is used for general construction and furniture, the tree is grown as an ornamental.

*Note.* *Michelia chapensis* is one of the widespread species in China. It is distinguished by glabrous leaves, petioles without scars, 6 tepals, and gynoecium generally hidden by the androecium. The taxa reduced above are essentially the same as *Michelia chapensis*. However, the gynoecium in *Michelia constricta*, *Michelia brachyandra*, and *Michelia nitida* is slightly exserted from instead of hidden within the androecium. *Michelia brachyandra* generally possesses a glabrous gynoecium, but sometimes it is hairy. Thus, usually the gynoecium of *Michelia chapensis* is glabrous. The length of the gynoecium varies from hidden to clearly exserted.

29. **Michelia leveilleana** Dandy, Kew Bull. 1927: 263. 1927. *Michelia cavaleriei* H. Léveillé, Feddes Repert. Spec. Nov. Regni. Veg. 9: 459. 1911, nom. illeg. non Finet & Gagnep. (1906). TYPE: *J. Cavalerie 3045* (holotype, E; isotypes, K, P). Figure 17.

*Michelia longipetiolata* C. Y. Wu ex Law & Y. F. Wu, Acta Bot. Yunnanica 10, 3: 336, t. 2. 1988. TYPE: *P. H. Yu 251* (holotype, PE).

Tree ca. 15 m by 30 cm diam.; young twigs slender, 2–3 mm diam., black-brown, appressed-tomentellous with straight, dark brown to rufous hairs, glabrescent, sparsely lenticellate; buds ovoid, ca. 1 cm long, rufous tomentose. Stipules glabrous to rufous tomentose, free from the petiole. Leaves coriaceous, dark green, glabrous above, pale green, at first rufous pubescent, later glabrescent beneath, elliptic, broadly elliptic, ovate, obovate, to narrowly obovate, 7.6–15 × 2.8–4.5 cm; apex acuminate or acute, acumen 5–10 mm long, base cuneate, broadly cuneate, obtuse, sometimes unequal; midrib impressed above, prominent below, nerves fine, somewhat obscure, more visible below than above, in 9–15 pairs, reticulation rather faint. Petiole minutely pubescent, glabrescent, 2.5–4.5 cm long, without stipular scars. Brachyblasts stout, tomentose with dark brown to rufous hairs, 5–10 × 4–5 mm, pedicles 4–6 mm long; bracts 2–3, tomentose with long, straight to undulate, dark brown

FIGURE 17. *Michelia leveilleana* Dandy. Branch with flower buds and fruit. Based on *W. C. Chen & C. T. Hwa 889* (K). Drawing by Joop Wessendorp, Rijksherbarium, Leiden.

hairs outside. Tepals 6, sometimes 4 or 7, white, glabrous, the outer 2–3 oblong to narrowly elliptic-oblong, 30–35 × 7–15 mm, the inner tepals elliptic to spathulate; stamens many, 12–15 mm long, connective appendage narrowly triangular, ca. 0.5 mm long, filaments 2–3 mm long, glabrous; gynoecium cylindric, 1–2 cm long, hidden by the androecium in bud but slightly longer than the androecium when flowers open; carpels many, tawny tomentellous; styles glabrous, ca. 1 mm long; gynophore tomentellous, 5–10 mm long; ovules more than 12 in each carpel; scars of perianth and stamens on torus 2–5 mm long. Fruiting brachyblasts 3 cm long. Fruits 7–9 cm long; gynophore 1–1.5 cm long, abortive carpels ca. 20; ripe carpels 7–10, ovoid, 12 × 9 mm, dark brown, lenticellate; scars of perianth and stamens 5–8 mm along the torus.

*Distribution.* CHINA. **Guizhou**: Bijie Xian, *Yu P.H. 251*; Leigongshan, *Li Y.K. 8879*. **Hubei–Sichuan, Metaseqoia area**: *Hwa C.T. 357*. **Hunan**: Dao Xian. **Yunnan**: Xiliang, *Dian Dongbei Exped. 754*; Zhenxiong, *Yu P.H. 1060*.

*Ecology.* In forest. Altitude: 1,000 m.

*Note.* After its publication by Dandy (1927), this species was never mentioned again in the literature. Type specimens of *Michelia leveilleana* bear flower buds and open flowers and possess obovate leaves. The type of *Michelia longipetiolata* only has fruits, and the leaves are broadly elliptic with relatively long petioles. Fortunately, we were able to study some collections (*C. T. Hwa 357*, *W. C. Cheng & C. T. Hwa 889, 938*), which were identified as *Michelia wilsonii* by S. Y. Hu, gathered from Hubei to Sichuan. These collections closely resemble the type of *Michelia leveilleana* and show the variations in shape and size of the leaves as well as length of the petioles, not only in different collections but within single specimens, e.g., *W. C. Cheng & C. T. Hwa 889*. Therefore, it is clear that these variations are continuous throughout the area of distribution. We conclude that all of these collections belong to a single species.

30. **Michelia martinii** (H. Lév.) Finet & Gagnep. ex H. Lév., Fl. Kouy Tchéou: 270. 1914. *Magnolia martini* H. Lév., Bull. Soc. Agric. Sarthe 59: 321. 1904. TYPE: *L. Martin & E. Bodinier 2066* (holotype, E; isotope, P).

*Michelia bodinieri* Finet & Gagnep., Bull. Soc. Bot. France 53: 1906. TYPE: *Farges 1324* (holotype, P).
*Michelia longistaminata* Law, Bull. Bot. Res. (China) 5(3): 122. 1985. TYPE: *S. P. Kuo 80358* (holotype, IBSC; isotype, BM).

Tree to 20 m high and ca. 50 cm diam.; bark gray, smooth; young twigs 2–4 mm diam., yellow-green to dull dark brown, smooth, glabrous to occasionally appressed-pubescent; old ones rough, sparsely lenticellate; buds ovoid or elliptic-ovoid, densely pubescent. Stipules densely pubescent with long, straight to slightly undulate, spreading, brownish or rarely gray hairs, free from the petiole. Leaves thinly coriaceous to coriaceous, dark green, glossy above, glabrous on both sides, elliptic-oblong, oblong, broadly to narrowly elliptic or narrowly obovate, 6.7–18 × 2–5.5 cm; apex short-acuminate to acute, base attenuate to cuneate or broadly cuneate; midrib impressed above, nerves fine, visible on both sides, more prominent below than above, in 7–17 pairs; reticulation laxly netted, conspicuous below. Petiole glabrous, 1.5–2 cm long, without scars. Brachyblast short and stout, 7–15 × 3–9 mm, densely pubescent with same indument as stipules, pedicle very short; bracts 3–6, densely pubescent outside. Flower bud ovoid to long-ovoid, 3–4.5 cm long; tepals 6(–8), white to yellow, glabrous or tomentose outside toward the base, subsimilar to unequal, the outer 3 broadly obovate, obovate-oblong, narrowly obovate to spathulate, 5–7 × 1.7–5 cm, the inner 3–4 smaller than the outer ones, broadly elliptic to narrowly oblong, short-clawed, 3–6 × 0.8–2.8 cm; stamens 8–25 mm long, connective appendage long-triangular, 0.5–2 mm long, filaments 3–7 mm long; gynoecium narrowly cylindric, glabrous, 8–18 mm long; gynophore glabrous, 6–12 mm long; carpels many, glabrous; ovules 10 or more in each carpel; scars of perianth and stamens on torus 2–5 × 5 mm. Fruiting brachyblast 13–14 × 4–9 mm, glabrescent. Fruit 6.5–10 cm long; ripe carpels dull brown, subglobose to ellipsoid, 1–16 × 4–11 mm. Scars of perianth and stamens 6–8 mm; gynophore under fruit ca. 15 mm long.

*Distribution.* China and Vietnam. In CHINA: **Guangdong**: Yuyuen, *Ko S.P. 52762*; Zhanjiang, *Nanzhidi 3719*. **Guangxi**: Huanjang, *Liang C.X. 77- 15*. **Guizhou**: Siuwen, *Tsiang Y. 8671*; Bijie, *Li Y.K. 11284*; Daping Xian, *Qian Bei Exped. 2250*. Henan. Southern Hubei. **Hubei–Szechwan, Metaseqoia area**: *Hwa C.T. 441*. **Sichuan**: Tchen Kéou Tin, *Farges R.P. 1394*; Mt. Omei, *Chow H.C. 8255*. **Yunnan**: Guangnan, *Wang C.W. 87594*; Mar li po, *Feng K.M. 13274*; Mengtze, *Henry A 11441*.

*Ecology.* In forests. Altitude: 1,000–2,000 m. Flowering February–March; fruiting August–September.

*Uses.* The flowers are extracted for volatile oil.

*Collector's notes.* Big tree, in mixed forests, on open hillside or near temples. Flowers fragrant.

*Note.* The type specimens of *Michelia bodinieri* and *Michelia longistaminata* strikingly resemble those of *Michelia martinii*. This species varies continuously throughout its range in texture of the leaves, width and length of brachyblasts, and length of stamens. The collections from Vietnam possess rigid coriaceous leaves, stout brachyblasts, and rather long stamens; the collections from Guangdong named *Michelia longistaminata* possess some extreme characters, such as thin leaves, thin brachyblasts, and rather long stamens. Because of the continuous variation, *Michelia longistaminata* is reduced here to *Michelia martinii*.

31. **Michelia xanthantha** C. Y. Wu ex Law & Y. F. Wu.

See under dubious species.

**4. Michelia** section **Micheliopsis** (Baill.) Dandy in Praglowski, World Pollen Spore Fl. 3: 5. 1974. *Magnolia* sect. *Micheliopsis* Baill., Adansonia 7: 4, 66. 1866. *Liriopsis* Spach,

Nat. Vég. 7: 460. 1839, non *Liriopsis* Reichenb. (1828). TYPE SPECIES: *Michelia figo* (Lour.) Sprengel.

Stipules adnate to the petiole, the latter short, not exceeding 10 mm. Bracts 3 (or occasionally 2 or 4). Tepals 6 or more, 3–4-merous, subsimilar. Usually shrubs or small trees. Fruits apocarpous.

32. **Michelia figo** (Lour.) Sprengel, Syst. Veg. 2: 643. 1825. *Liriodendron figo* Lour., Fl. Cochinch.: 347. 1790. *Magnolia figo* (Lour.) DC., Syst. Nat. 1: 460. 1817. TYPE: *Loureiro s.n.* not seen.

*Magnolia fuscata* Andr., Bot. Repos. 4: t. 229. 1802. *Michelia fasciata* Vent., Jard. Malmaison: t. 24, 1803, nom illeg. *Magnolia versicolor* Salisb., Parad. Lond. 1(1): t. 5. 1806, nom. illeg. *Magnolia meleagrioides* Hort. ex DC., Syst. Nat. 1: 458. 1817, nom. illeg. *Michelia fuscata* (Andr.) Blume ex Wall., Cat.: no. 6495. 1832. *Liriopsis fuscata* (Andr.) Spach. Hist. Nat. Vég. 7: 461. 1839. TYPE: Andrews (1802, t. 229).

*Magnolia annonaefolia* Salisb., Parad. Lond. 1(1): t. 5. 1806. *Magnolia fuscata* var. *annonaefolia* (Salisb.) DC., Syst. Nat. 1: 458. 1817. TYPE: Salisbury (1806, t. 5).

*Magnolia fuscata* var. *hebeclada* DC., Syst. Nat. 1: 458. 1817. TYPE: Mauritius, *Thouars s.n.* not seen.

*Michelia parviflora* Deless., Icon. Sel. Pl. 1: 22, t. 85. 1821, nom. illeg., non *Michelia parviflora* DC. (1817). *Magnolia parvifolia* DC., Syst. Nat. 1: 459. 1817. *Magnolia parviflora* Blume, Bijdr.: 9. 1825. *Magnolia fuscata* var. *parviflora* (Blume) Steud., Nomencl. Bot. ed. 2, 2: 89. 1841. *Sampacca parviflora* (Deless.) Kuntze, Revis. Gen. Pl. 1: 6 (as *S. parvifolia*). 1891. *Michelia parvifolia* (DC.) B.D. Jacks., Index Kewensis 2: 223. 1894. TYPE: *Herb. Delessert* (holotype, G-DEL not seen).

*Michelia skinneriana* Dunn, J. Linn. Soc. Bot. 38: 354. 1908. TYPE: *Hongkong herb. 2448* (holotype, HK; isotype, A).

*Michelia amoena* Q. F. Zheng & M. M. Lin, Bull. Bot. Res. (China) 1: 63, t. 1987. TYPE: China. Fujian: Chang-Ting, 700 m, *Q. F. Zheng & Lin 84504* (in herb. Fujian Forestry College).

*Michelia brevipes* Y. K. Li & Wang, Acta Phytotax. Sin. 25, 5: 408, t. 1. 1987. TYPE: China. Guizhou: Longtoudashan, Anlong, *C. Z. Dang 913* (HGAS not seen).

32a. **Michelia figo** var. **figo.**

Shrub to small tree to 15 m high and 30 cm diam.; bark gray; young twigs slender, 1–2 mm diam., brown gray, purple-brown, pubescent with short, straight hairs, glabrescent, the indument at first brown, later dark brown to gray; old twigs white-gray to purple-brown, irregularly longitudinally fissured. Stipules densely pubescent or tomentose, adnate to the petiole, scars to half of its length, 2–3 mm long. Leaves chartaceous to thinly coriaceous, dark green, glossy, glabrous or rather sparsely scattered-pubescent above, light green, appressed-pubescent with short to long, straight to slightly undulate, brown to dark brown hairs, glabrescent beneath, obovate-elliptic to narrowly obovate-elliptic or elliptic to broadly elliptic, occasionally subrhombic, 2–12(–17) × 1.5–4.5 cm; apex subcaudate, acuminate, acumen 5–20 mm long, sometimes acute, base cuneate to obtuse; midrib slightly impressed toward the base, densely pubescent, glabrescent above, prominent, densely long-pubescent, glabrescent beneath, nerves obscure on both sides, in 7–12 pairs, reticulation lax, hardly visible on both sides. Petiole densely spreading-pubescent, 3–5 mm long, scarred. Brachyblast densely spreading-pubescent, variable in length and width, 4–20(–27) × 2–4 mm, pedicle absent; bracts ca. 3, densely pubescent or tomentose outside. Flower bud ovoid to ellipsoid, 1.5–2 cm long; flower sweet-scented, white or yellow, often tinged with purple, sometimes purplish; tepals 6, subsimilar, fleshy, glabrous, oblong-obovate, obovate to spathulate, 1.5–2.5 × 0.6–1.2 cm; stamens 7–11 mm long, connective appendage triangular, 0.5–1 mm long, filaments glabrous, 1.5–3 mm long; gynoecium subcylindric, exceeding above the androecium, 2–11 mm long; gynophore pubescent with spreading, yellow to brown hairs, occasionally glabrous, 1–3 mm long; carpels many, glabrous or tomentellous; scars of perianth and stamens on torus 1–3 mm long. Fruiting brachyblast 7–20(–27) × 2–4 mm. Fruit 1–5 cm long; ripe carpels 1–15, subovoid to subglobose, black-brown to brown, ± pubescent, with a ca. 1-mm-long beak at apex, 7–12 × 7–9 mm; gynophore 2–11 mm long; scars of perianth and stamens 2–5 mm long.

*Distribution.* Southeastern CHINA. **Anhui**: Fujian, Amoy, Nanputo, *Chung H.H. 5921*; Buon Kang, *Chung H.H. 3374*; Foochow, *Tang S.G. 7167*; Hok Chang, *Tang S.G. 16106*; Kiuliang, *Chung H.H. 6815*. **Guangdong, Guangzhou, on hills**: *Chow K.S. 145*; Kau Fung, Loh Chang Distr., *Tsang W.T. 20992*; Lofoushan, *Chun N.K. 40574*; Ngok Shing Shan, *Taam Y.W. 542*; Pan Ling Tsze, *Chun W.Y. 5856*. **Guangxi**: Tung Hoo, *Ching R.C. 5613*; Baishou, *Li Z.J. 653*; Lingui, *Huang S.L. 2000014*; Longsheng, *Qin H.F. 70033*; Xingan, *Chen Z.Z. 51516*. **Jiangxi**: Dagangshan, *Yao Kan 9283*; Kouyang, *Tsiang Y. 10012*; Sai Hang Cheung, *Lau S.K. 4047*; Yi Feng, *Hsiung Y.K. 6307*. **Zhejiang**: Nan Hoo, *Hu H.H. 190*; Ping Yung, *Ching R.C. 1986*. Widely cultivated in most of China and other warm parts of the world.

*Ecology.* In forests. Altitude: 60–1,000 m. Flowering March–May; fruiting July–August.

*Collector's note.* Flowers sweet-scented, odor detected at a distance.

*Uses.* Flowers used for perfuming tea; leaves for volatile oil and medicinal purposes; shrub grown as an ornamental.

*Note.* No original Loureiro specimen has been traced. However, there is no doubt that this is the plant described by Loureiro as *Michelia figo.*

The species varies greatly in the following characters: size and shape of the leaves, length and width of the brachyblast, size and color of the flowers, and the indument of the carpels. For example, the carpels usually are glabrous, but a continuous variation of the indument of the carpels can be observed throughout its distribution.

None of the type specimens or other collections of *Michelia amoena* and *Michelia brevipes* were available for study. We consider both as synonymous with *Michelia figo,* according to their description and the published figures.

Sometimes abnormalities are found, such as leaf-like bracts, more-flowered brachyblasts, terminal unibracteate flowers, and carpellody of the inner stamens.

32b. **Michelia figo** var. **crassipes** (Law) B. L. Chen & Nooteboom, stat. nov. *Michelia crassipes* Law, Bull. Bot. Res. (China) 5(3): 121, t. 1. 1985. TYPE: China. Guangdong: Lechang, 1,000 m, *S. H. Chun 3115* (holotype, IBSC not seen).

Shrub or small tree, 2–5 m high; bark gray-brown; buds, young twigs, stipules outside, petiole and brachyblasts densely pubescent with long, tawny or rufous hairs. Young twigs 2–3 mm diam. Stipules adnate to very high on the petioles, scars to whole length of the petioles. Leaves thinly coriaceous, dark green, glossy, glabrous above, pale green, at first brown to rufous tomentose everywhere, especially long-hairy on the veins, later glabrescent beneath, obovate or narrowly obovate, rarely narrowly elliptic, 7–13 × 2.5–4 cm; apex short- or long-acuminate, base cuneate to broadly cuneate; nerves fine, in 6–9 pairs. Petiole 2–4 mm long. Brachyblasts stout and short, 3–4 mm long, flowers heavily scented, purple-red to dark purple; tepals 6, subsimilar, long-elliptic, 18–20 × 6–8 mm; stamens ca. 1 cm long; gynoecium short-cylindric, densely pubescent, shorter than the androecium, ca. 8 mm long; gynophore ca. 2 mm long; carpels ovoid, densely tomentellous, 3.5–5 mm long; styles ca. 2 mm long. Fruits 2.5–5 cm long; ripe carpels compressed ovoid to subglobose, glabrescent, papilliferous; fruiting brachyblasts stout and short, 10–20 × 3–5 mm.

*Distribution.* CHINA. **Northern Guangdong**: *Chen B.L. 81007, Zheng P. 10406.* **Northeastern Guangxi**: Ruyuan, *Chen B.L. 81006*; Jinxiu Xian, *Pen Z.H. 51279.* Also in southern Hunan.

*Ecology.* In forests. Altitude: 300–700 m. Flowering April–May; fruiting August–September.

*Note. Michelia crassipes* is treated as a variety of *Michelia figo* because there are few vegetative characters to separate the two. However, the tepals are purple, the brachyblast is stout, and the gynoecium is shorter than the androecium in *Michelia crassipes. Michelia figo* has white to yellow flowers with purple, short to long, slender brachyblasts, and the gynoecium exceeding the androecium. We observed that the flowers are variable when *Michelia crassipes* is cultivated in Guangzhou, e.g., brachyblasts become slender, the tepals are rose to pale rose instead of purple, the gynoecium is longer than the androecium. In cultivation the flowers of *Michelia crassipes* become more or less like those of *Michelia figo.* Therefore, we consider *Michelia crassipes* to be a wild strain of *Michelia figo.*

33. **Michelia yunnanensis** Franchet ex Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 43, t. 6A. 1905. TYPE: *Delavay 4848* (holotype, P; isotypes, E, K).

*Michelia yunnanensis* Franchet ex Finet & Gagnep. var. *angustifolia* Finet & Gagnep., Bull. Soc. France (Mémoires) 4: 44, t. 6B. 1905. TYPE: *Bodinier & Ducloux 168* (holotype, P; isotypes, BM, K).

*Michelia dandyi* Hu, Bull. Fan. Mem. Inst. Biol. (Peiping) 8: 34. 1937. TYPE: *H. T. Tsai 53380* (holotype, PE; isotype, A).

Shrub to small tree, 6–12 m high; buds, young twigs, stipules outside, young leaves beneath, petiole, brachyblast, bracts outside, gynophore and carpels appressed- to spreading-tomentose or pubescent with short to long, straight to slightly undulate, brown, rufous, black-brown to gray hairs; young twigs 1.5–2 mm diam., olive-green, gray-brown to purple-brown. Stipules adnate to nearly the whole length of the petiole, stipular scars 3–7 mm long. Leaves membranous to coriaceous, bright green, ± brown pubescent, glabrescent above, greenish, at first densely or sparsely pubescent, finally glabrescent beneath, obovate or narrowly obovate to elliptic, 2–10 × 1–4 cm; apex obtuse or rounded, or acute to short-acuminate, occasionally retuse, base cuneate to obtuse; midrib slightly impressed, densely pubescent, especially

toward the base above, prominent, densely or sparsely pubescent, glabrescent beneath, nerves obscure or visible on both sides, in 7–9 pairs, reticulation faint on both sides when dry. Petiole stout, 5–10 mm long. Brachyblast 4–9(–14) × 2–2.5 mm, pedicle absent; bracts 3. Flower bud ovoid to narrowly ovoid, 2–3 cm long; flower heavily scented; tepals 6–12(–17), white, yellowish white to greenish white, subsimilar, the outer 3–4 obovate, broadly obovate to obovate-elliptic, abruptly constricted near the base, becoming rather short-clawed, glabrous to tomentellous outside at the base, 2.2–3.5 × (0.8–)1.4–1.8 cm, the inner 3–8 obovate, oblong to subspathulate, 2–2.2 × 0.9–1.2 cm; stamens 5–10 mm long, connective appendage very short-triangular or semiorbicular, 0.5–1 mm long, filaments 2–3 mm long; gynoecium subovoid to oblong, longer than the androecium, 3–5 mm long; gynophore 5–8 mm long; carpels ca. 15 or fewer; ovules 3–8; scars of perianth and stamens on torus 0.5–3 mm long. Fruiting brachyblast 4–9 × 2–3 mm. Fruit 1–4.5 cm long; ripe carpels 1–8, subglobose, dull brown, ± pubescent, lenticellate, sessile, apically with a 1–1.5 mm long beak, 7–14 × 7–12 mm; gynophore 7–10 mm long; scars of perianth and stamens 2–5 mm long. Seeds 1–2 in each carpel, ellipsoid to ovoid, 6–8 × 5–7 mm.

*Distribution.* CHINA. **Guizhou**: Anlong Xian, *Dang C.Z. 886*. **Sichuan**: between Yimen and Pai kuo wan, *Schneider C. 607*. **Yunnan**: Likiang snow range, *Rock J.F. 10661*, *Wang C.W. 70468*; Juanchiang, *Henry A 13277*; Kunming, *Sino-Amer. Bot. Exped. 1413*; Mar li po, *Feng K.M. 12636*; Mengtze, *Henry A 9429*.

*Ecology.* In forest or thickets. Altitude: 1,100–2,300 m. Flowering March–April; fruiting August–September.

*Uses.* Flowers and leaves are used as spices; the tree is grown as an ornamental.

*Note.* *Michelia yunnanensis* varies in shape and size of the leaves. Although variety *angustifolia* has relatively narrow and small leaves, intermediate forms can be found throughout the range. *Michelia dandyi* is similar to *Michelia yunnanensis*.

**5. Michelia** section **Tsoongiodendron** Nooteboom & B. L. Chen. *Tsoongiodendron* W. Y. Chun, Acta Phytotax. Sin. 8: 7. 1963. TYPE SPECIES: *Tsoongiodendron odorum* Chun = *Michelia odora* (Chun) Nooteboom & B. L. Chen.

Stipules adnate to the petiole. Tepals 9, subsimilar. Fruits syncarpous, very large; follicles crowded, sessile, woody, large, without a beak, rounded on the back.

34. **Michelia odora** (Chun) Nooteboom & B. L. Chen, comb. nov. *Tsoongiodendron odorum* Chun, Acta Phytotax. Sin. 8, 4: 281, 9 tt. 35, 36. 1963. TYPE: *S. P. Ko 51928* (holotype, IBSC; isotype, BM not seen).

Tree to 25 m high and 1 m diam.; bark grayish brown, deeply wrinkled; buds, stipules outside, young twigs, leaves beneath (especially on the midrib and nerves), petiole, brachyblast, bracts outside, gynophore and carpels densely covered with an indument of short to long, straight to undulate, spreading, yellowish to brown or clear hairs; young twigs 2–3 mm diam., dull black-brown; old ones gray-brown, longitudinally wrinkled, irregularly transverse-fissured, lenticellate. Stipules adnate to the petiole from the lower base to its middle or higher, stipular scars 6–18 mm long. Leaves thinly coriaceous, green, glossy, glabrous but densely pubescent on the midrib above, greenish beneath, elliptic or narrowly to broadly obovate-elliptic, 8–20 × 3.5–7 cm; apex short-acuminate, occasionally acute, base cuneate to rounded; midrib slightly impressed above, conspicuously elevated below, nerves in ca. 12 pairs, hardly visible above, reticulation laxly netted, prominent beneath. Petiole 0.9–3 cm long. Brachyblast 7–10 × 2–3 mm, pedicle absent, bracts 2–3. Flower white to yellowish, very fragrant; tepals 9, subsimilar, narrowly obovate-elliptic, the outer three, 17–20 × 6.5–7.5 mm, the innermost tepals three, ca. 15–16 × 5 mm; stamens 40–45, 7.5–8.5 mm long, connective appendage very short, ca. 0.5 mm long, filaments 1.5–3 mm long; gynoecium subovoid, 3–4 mm long, shorter than androecium; gynophore stout, 2–2.5 × 1–2 mm; carpels 10–12, narrowly ovoid; styles glabrous, ca. 2 mm long. Fruiting brachyblast 1–2 × 1–1.3 cm. Fruit syncarpous, long-elliptic, sometimes subglobose because of the abortion of the upper carpels, 13–16 × 7–9 cm; ripe carpels crowded, sessile, woody, large, without a beak, 4–6 cm long; the exocarp thin and fleshy, olive-green, white lenticellate, dark brown and yellow-dotted when dry, mesocarp woody, 1–2 cm thick, endocarp thin, greenish yellow. Seeds 4–6 in each carpel, ellipsoid to irregularly shaped, ca. 15 × 8 mm.

*Distribution.* China and northern Vietnam. In CHINA. **Fujian**: Jing Xian, *Ye G.D. 1690*. **Guangxi**: Longjin, *Tam P.C. 57604*. **Guangdong**: Lockchong distr., *Ko S.P. 51109*. **Hainan**: *Chun N.K. & C.L. Tso 44257*. Also in southern Jiangxi and southeastern Yunnan.

*Ecology.* In forest. Altitude: 500–1,000 m. Flowering March–April; fruiting September–October.

*Uses.* Wood white, straight-grained, fine-textured, light and hard; used for furniture, building, plywood, musical instruments, and work not in contact with the soil; tree grown as an ornamental.

*Collector's note.* Flower light red.

*Note.* This species is characterized by very small flowers and huge syncarpous fruits. Its leaves are easily confused with those of *Michelia balansae*, which has, however, free stipules.

Dandy (ex Gagnepain, 1938) already mentioned the species as a nomen nudum, *Michelia gravis*.

**6. Michelia** section **Paramichelia** Nooteboom & B. L. Chen, stat. et sect. nov. *Paramichelia* H. H. Hu, Sunyatsenia 4: 142. 1940. TYPE: *Paramichelia baillonii* (Pierre) Hu = *Michelia baillonii* (Pierre) Finet & Gagnep.

Stipules adnate to the whole length or almost the whole length of the petiole. Bracts 3. Tepals 12, 4-merous, subsimilar. Fruits syncarpous.

35. **Michelia baillonii** (Pierre) Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 46. 1905. *Magnolia baillonii* Pierre, Fl. Forest. Cochinch. 1: t. 2. 1880. *Paramichelia baillonii* (Pierre) Hu, Sunyatsenia 4: 144. 1940. TYPE: *Pierre 750* (holotype, A; isotype, K).

*Talauma spongocarpa* King, Magnol. Brit. India 3: 205, t. 47 bis. 1891. *Aromadendron spongocarpum* (King) Craib, Fl. Siam 1: 25. 1925. TYPE: *Calcutta Botanic Garden collector* (*Badal Khan*) *102* (holotype, CAL; isotype, L).

*Talauma phellocarpa* King, Magnol. Brit. India 3: 205, t. 47 ter. 1891. *Michelia phellocarpa* (King) Finet & Gagnep., Bull. Soc. Bot. France (Mémoires) 4: 44. 1905 TYPE: *Peal s.n.* (holotype, CAL; isotypes, BM, L, US).

Huge tree to 50 m high and 1 m diam.; young twigs slender, 2–3 mm diam., dull brown, densely pubescent with long, straight to slightly undulate, ± spreading, yellowish to brownish hairs; old ones black-brown, sparsely white lenticellate. Stipules densely pubescent with same hairs as the young twigs, adnate to the petiole nearly to half its length, scars 6–10 mm long. Leaves chartaceous, above dark green, appressed-pubescent with slender, straight, clear to yellowish hairs, brown pubescent on the midrib when young, glabrescent when old, below pale green, pubescent with short and long to rather long, straight to undulate, yellowish to brownish hairs at first, finally glabrescent, narrowly obovate, obovate, obovate-elliptic to narrowly elliptic, usually somewhat unequal, 6–16.5(–23.5) × 3–8.5 cm; apex short-acuminate to acute; base cuneate or broadly cuneate, sometimes rounded; midrib impressed above; nerves fine, obscure above, visible beneath, in 9–15 pairs; reticulation rather densely netted, faint on both sides when dry. Petiole densely pubescent, glabrescent, 1.5–3.5 cm long. Brachyblast slender to stout, 8–14 × 2–3 mm, yellowish tomentose, pedicle absent; bracts 3, densely yellowish or brown tomentose outside. Flower bud ovoid-cylindric, 2.7–3 mm long; flower heavily scented; tepals 12–18(–20), white or yellow-white, subsimilar, spathulate to obovate-linear, glabrous to pubescent outside toward the base, apex acuminate to acute, base attenuate to the base, usually becoming long-clawed, 23–35 × 2.5–7 mm; stamens 7–9 mm long, connective appendage narrowly triangular, 1–2 mm long, filaments glabrous, 1–2 mm long; gynoecium ovoid-cylindric, 6–9 mm long, longer than the androecium; gynophore yellow pubescent, 3–4 mm long; carpels densely yellow pubescent; styles red, glabrous; scars of perianth and stamens on torus 5–7 × 7–11 mm. Fruiting brachyblast dull black-brown, ± pubescent, 1–2 × 0.6 cm. Fruit syncarpous, ovoid, ovoid-ellipsoid, to irregularly shaped, dull gray-black, densely lenticellate outside, 3–9 × 2.5–4.5 cm; ripe carpels connate, falling off when maturing in irregular masses, midrib lignified and persistent in the form of an upcurved laterally compressed hook; gynophore 7–13 × 5–9 mm; scars of perianth and stamens 5–7 × 7–11 mm. Seeds subovoid, cordate to irregularly shaped, 7–10 × 6–7 mm.

*Distribution.* Assam, China, Thailand, Burma, Vietnam, and Cambodia. In CHINA. **Southern Yunnan**: Chenkang, Maliling, *Yu T.T. 17395*; Che-li Hsien, *Wang C.W. 78590*; Fo-Hai, *74653*; Lincang, *Xin J.S. 383*; Menglian Xian, *Menglian Exped. 10145*; Xishuang Banna, *Sino-Rossica Exped. 5627*.

*Ecology.* In forest. Altitude: 300–1,600 m. Flowering February–March; fruiting August–September.

*Uses.* Wood straight-grained, fine-textured, and durable; used for building, bridges, furniture, interior finish, and plywood.

*Collector's note.* Trees in mixed forests or thickets, fruits green-black, seeds with red aril.

*Note.* This species has not only a wide distribution, but also a considerable variation in shape and size of the leaves.

Hu (1938) named this species *Aromadendron yunnanensis*, nom. nudum.

DUBIOUS SPECIES

**Michelia chongjiangensis** Y. K. Li & X. M. Wang, Guizhou Sin. 3: 18. 1983. TYPE: China. Guizhou: Taiyangsun, Chongjiang, 1,300 m, *Y. K. Li 9294* (HGAS not seen) = *Michelia ?leveilleana* Dandy.

**Michelia caloptila** Law & Y. F. Wu, Bull. Bot. Res. (China) 4(2): 152, t. s.n. 1984. TYPE: China. Jiangxi: Zixi, *Jiangxi gong-da linxue-xi 80069* (IBSC not seen).

**Michelia elegans** Law & Y. F. Wu, Bull. Bot. Res. (China) 8(3): 71, t. 1. 1988. TYPE: China. Guangzhou: South China Botanic Garden, 27 Apr. 1986, *Y. W. Law 6109* (IBSC not seen) = *Michelia ?cavalerieri* Finet & Gagnep.

**Michelia laevifolia** Law & Y. F. Wu, Bull. Bot. Res. (China) 8(3): 72, t. 2. 1988. TYPE: China. Guizhou: Anlong, 1,500 m, 22 June 1960, *T. S. Chang 4852* (IBSC not seen) = *Michelia ?yunnanensis* Franchet ex Finet & Gagnep.

**Michelia sphaerantha** Z. S. Yue, Acta Bot. Yunnanica 9(4): 413, t. 1, 1987. SYNTYPES: *Z. S. Yue 83-111, 86-107* (KUN not seen).

*Note.* Yue meant to describe *Michelia sphaerantha* C.Y. Wu (in manuscript), later again published by Wu in Acta Bot. Yunnanensis 10: 335. 1988, nom. illeg., with another type. The latter is *Michelia masticata*. According to the drawing published by Yue and a leaf fragment we received from him, it appears that *Michelia sphaerantha* Z. S. Yue is a different species: it has its stipules adnate to the petiole. Study of the type is necessary to conclude its status.

11. **Michelia fujianensis** Q. F. Zheng, Bull. Bot. Res. (China) 1(3): 92, t. 1981. TYPE: China. Fujian: Sanming Shi, *K. R. Wu 79100* (in herb. Fujian Forestry College not seen).

Tree to 15 m, ca. 40 cm diam.; bark gray-brown to dark brown, smooth or slightly rough; buds, young twigs, petioles, and brachyblasts densely pubescent with gray or brown hairs. Stipules free from the petiole. Leaves thinly coriaceous, pubescent, glabrescent, especially on the midrib above, densely brown appressed-pubescent beneath, oblong to narrowly ovate-elliptic, 6–11 × 2.5–4 cm; apex acuminate to acute, base cuneate to obtuse; midrib prominent below, nerves prominent on both sides, in 8–9 pairs. Petiole 1–1.5 cm long. Brachyblast ca. 5 mm (15 mm?) long; bracts densely brown pubescent. Flower bud ellipsoid-ovoid, ca. 1.5 × 0.8–1 cm; tepals ca. 15 mm long, anthers ca. 5 mm long; gynoecium ovoid; gynophore densely pubescent with long hairs, ca. 2 mm long; carpels ca. 20 or more, gray pubescent. Fruiting brachyblast 5 mm long. Fruit ca. 3 cm long; ripe carpels 1–4, ovoid to subglobose, 1–1.5 cm long, short-stipitate.

*Distribution.* CHINA. **Fujian**.

*Ecology.* In forest. Altitude: below 500 m. Flowering February–April; fruiting August–October.

*Note.* The original description only mentioned "fruiting brachyblast 5 mm long." Later, Lin (1985) described "brachyblast stout, ca. 15 mm long" and "fruiting brachyblast 5 mm long." Obviously the length of the brachyblast was misrepresented by him.

We had no opportunity to study collections of *Michelia fujianensis*, but it seems closely allied with and might be conspecific to *Michelia cavaleriei*, especially in number of tepals and length of fruit, which are variable in that species.

8. **Michelia flaviflora** Law & Y. F. Wu, Acta Bot. Yunnanica 10(3): 340, t. 6. 1988. TYPE: *H. Wang 100120* (IBSC not seen).

Tree to ca. 15 m high; buds, young twigs, stipules, petiole, and brachyblasts yellowish tomentose; young twigs brown tomentellous; old ones white lenticellate. Stipules free from the petiole. Leaves thinly coriaceous, dark green, glabrous above, glaucous, brown sericeous beneath, narrowly elliptic or obovate-elliptic, 15–24 × 3.6–5.5 cm; apex acuminate, base cuneate; midrib slightly prominent to impressed above, nerves fine, in 16–24 pairs. Petiole dilatate toward the base, without scars, ca. 0.5–1.2 cm long. Brachyblasts ca. 1 cm long. Tepals 15, yellow, subsimilar; stamens ca. 90, 1.1–1.5 cm long, connective appendage triangular, 1–2 mm long; gynoecium narrowly ovoid, ca. 1.2 cm long, exceeding beyond the androecium; gynophore tomentellous, ca. 1 cm long, ovaries ovoid, densely villous, 4 mm long; styles glabrous, ca. 2 mm long.

*Distribution.* Vietnam and China. In CHINA. **Yunnan** (Pingbian).

*Note.* There was no material of *Michelia flaviflora* available. In Law's description, no dimensions of the flowers were given, but we think it represents a distinct species.

21. **Michelia shiluensis** Chun & Y. Wu, Acta Phytotax. Sin. 8(4): 286. 1963. TYPE: *Hainan Exped. 90669* (IBSC not seen).

Tree to 18 m high and 30 cm diam.; bark gray; twigs, leaves, and petiole glabrous; young twigs slightly black, smooth; old ones dull gray to purple-brown, somewhat rough, longitudinally striped and lenticellate; terminal buds narrowly ellipsoid, orange or gray sericeous, glabrescent, 10–12 × 4–5 mm. Stipules pubescent, free from the petiole. Leaves coriaceous, ± rigid, dark green above, paler green beneath, obovate, obovate-oblong, 8–14(–20) × 4–7(–8) cm; apex acute, base attenuate to cuneate or broadly cuneate; midrib impressed above, nerves in 8–12 pairs, reticulation densely netted, both nerves and reticulation conspicuously visible on both sides when dry. Petiole wide sulcate above, 1–3 cm long, without scars. Brachyblast ca. 1.7 cm long. Flowers white, cup-shaped; tepals 9, fleshy, obovate, convex outside, 3–4.5 × 1.5–2.5 cm; stamens 2–2.5 cm long, anthers 12–17 mm long, filaments reddish; gynoecium pubescent, 1.4–2.1 cm long; carpels many (ca. 25 or more), ovoid, 2.5–4 mm long; styles ca. 1.5 mm long. Fruiting brachyblast with 2–3 bract scars. Fruits 4–5 cm long, peduncles ca. 2–3 cm long; carpels usually partly fertile; ripe carpels obovoid or obovoid-ellipsoid, 8–12 mm long, short-beaked at the apex. Seeds broadly ellipsoid, ca. 8 × 6 mm.

*Distribution.* CHINA. **Hainan** (Dingfang, Baoting).

*Ecology.* In evergreen broad-leaved forests. Altitude: 200–1,500 m. Flowering March April; fruiting June–August.

*Uses.* Wood straight-grained, even and fine-textured, slightly heavy, with a characteristic odor and durable; used for furniture, musical instruments, and building; the tree is grown as an ornamental.

*Note.* No collections could be consulted, but this is probably a good species. However, the original description does not give enough key characters.

31. **Michelia xanthantha** C. Y. Wu ex Law & Y. F. Wu, Acta Bot. Yunnanica 10(3): 338, t. 4. 1988. TYPE: *Sino-Ussr Exped. 7046* (KUN not seen).

Tree to 30 m high and 1 m diam.; buds cylindric, glabrous, ca. 1.5 cm long; young twigs dark brown to gray-yellow, ca. 4.5 cm diam., sparsely lenticellate. Stipules glabrous, free from the petiole. Leaves thinly coriaceous, oblong to obovate-oblong, 15–17 × 6.2–7.5 cm; apex short-acuminate, base cuneate to rounded; glabrous on both sides; midrib slightly impressed above, prominent beneath; nerves in 11–18 pairs, reticulation prominent on both sides. Petiole without stipular scars, 2–2.5 cm long. Brachyblast glabrous, ca. 1.5 cm long. Tepals 6, yellow, fragrant, subsimilar, narrowly oblong or narrowly obovate, 4–5.5 × 1–1.5 cm; stamens 2.3–2.5 cm, anthers 1.8–2 cm long, filaments ca. 3 mm long, connective appendage short-triangular, 1–2 mm long; gynoecium cylindric, 1.8–2 cm long; gynophore 2–3 cm long; carpels many, ovate, densely gray pubescent, 3–4 mm long; styles ca. 1 mm long. Fruit pendent, ca. 21 cm long; ripe carpels dark gray-brown, sparsely lenticellate.

*Distribution.* CHINA. **Yunnan** (Xishuangbanna).

*Ecology.* In forests. Altitude: 1,350 m.

*Note.* We were not able to study the type specimen of *Michelia xanthantha*. However, based on the description this seems to be a good species.

**MAGNOLIACEAE** subfamily **LIRIODENDROIDEAE** (Barkley) Law Yuh-wu, Acta Phytotax. Sinica 22: 105. 1984. Liriodendraceae Barkley, Phytologia 32: 304. 1975.

Leaves 2–10(usually 4–6)-lobed, the apex truncate or widely emarginate; stipules always free from the petiole. Anthers extrorse. Fruiting carpels woody, indehiscent, samaroid, produced at the apex into a long winglike beak, indehiscent, caducous. Testa adherent to the endocarp.

One genus:

V. **Liriodendron** L., Sp. Pl.: 535. 1753. TYPE SPECIES: *Liriodendron tulipifera* L.

*Tree.* Leaves deciduous. Flowers terminal, solitary, bisexual. Tepals 9–17, 3-merous, subequal. The connective produced into a short appendage. Gynoecium sessile. Carpels numerous, free, the lowermost sterile. Ovules 2. Seeds 1–2 in each carpel.

*Distribution.* Two species, southeastern Asia and southeastern North America.

1. **Liriodendron chinense** (Hemsley) Sarg., Trees & Shrubs 1: 103 t. 52. 1903. *Liriodendron tulipifera* L. var.? *chinense* Hemsley, J. Linn. Soc. Bot. 23: 25. 1886. SYNTYPES: *Shearer s.n.* (1875), *Maries s.n.* (1877) not seen.

Tree to 40 m high, 1 m or more diam.; young twigs 2–4 mm diam., gray, gray-brown, dull brown to purple-brown, glaucescent, old ones dull purple or gray-black, lenticellate. Stipules yellow to brownish, glabrous, free from the petiole. Leaves mem-

branaceous to chartaceous, (3–)5.5–12(–18) × 3–9.5(–23) cm; apex 2-lobed, with a pair of lateral lobes near the base; glabrous on both sides, bright green above, glaucescent to glaucous beneath; midrib elevated beneath, nerves rather prominent below, in 5–7 pairs. Petiole slender, glabrous, 2.5–8 cm long. Peduncle glabrous, 8–9 × 3–4 mm; bract single. Flower bud ovoid, 4.5–7 cm long; flower cup-shaped; tepals 9, subsimilar, greenish to yellowish, the outer 3 calycoid, glabrous, obovate to obovate-elliptic, abruptly constricted near the base and becoming short-clawed, 2.5–4.5 × 1.5–2 cm, the inner tepals 6, erect, obovate, 3–4 cm long, lengthwise yellow-striate outside; stamens 20–22 mm long, connective appendage triangular, short, filaments 6–8 mm long; gynoecium ovoid-cylindric, ca. 7 × 6 mm, carpels yellow-green; scars of perianth and stamens on torus ca. 3 × 5 mm. Fruiting peduncle 1–1.6 × 0.3–0.5 cm. Fruit ovoid, 4.5–9 × 2 cm, ripe carpels samaroid nutlets, 2–3 × 0.4–0.6 mm.

*Distribution.* CHINA. **Anhui**: Huangshan, Bai Zhang Tan, *Deng & Yao 79147*. **Zhejiang**: Hangchow, *Chiao C.Y. herb. no. 18844*. **Guangxi**: Guanyang, *Chen Z.Z. 52523*; Xingan Xian, *Yu S.L. 900086*. **Guizhou**: Libo, *Huang D.F. 1623*; Fanchingshan, *Chen J.C. 745*. **Hunan**: Dao Xian, *Yu S.L. 61528*. **Hubei**: Chienshih Hsien, *Chow H.C. 1094*. **Jiangsu, Nanjing**: *Chang H.T. 5396*. **Jiangxi**: Lushan, *Chang H.T. 5309*; Kuling, *Chiao C.Y. herb. no. 18560*. **Sichuan**: Hsiu-shan-hsien, *Tu & Sun 4070*. **Yunnan**: Sichour Hsien, Shiangpyng-shan, *Feng K.M. 11447*; Kunming, *Chang H.T. 5094*. Also in southern Shaanxi and cultivated in Taiwan and North Vietnam.

*Ecology.* In mixed forests, growing particularly well on sandstone, granite, and sandshale formations. Altitude: 500–1,700 m. Flowering May; fruiting September–October.

*Uses.* Wood reddish brown, fine-textured and straight-grained, used for furniture; bark for medicinal purposes; because of the shape of leaves, this is an especially ornamental tree.

*Collector's notes.* Tree, growing along sandy or rocky slopes, sometimes by roadsides and streams; bark pale gray; stipules tinged red at apex; flowers yellowish; fruits green when young, brown later.

*Note.* Finet & Gagnepain (1905) treated this species as *Liriodendron tulipifera* L.

2. **Liriodendron tulipifera** L., Sp. Pl. 1: 535. 1753 [*Tulipifera virginiana* Hermann, Hort. Ludg.-Bat. Cat.: 612, t. 613. 1687]. *Liriodendron procerum* Salisb., Prodr. Stirp. Chap. Allerton: 379. 1796. *Liriodendron truncatifolium* Stokes, Bot. Mat. Med. 3: 233. 1812. TYPE: t. 613 (P. Hermann, 1687).

Tree to 60 m high, 3.5 m diam.; bark deep longitudinally fissured; brown to purple, often pruinose. Leaves ca. 7–12 cm long; apex 2-lobed, with 2–3 lateral lobes, minutely white hairy when young, soon glabrous beneath. Petiole ca. 5–10 cm long. Flowers cup-shaped, tepals 9, outer tepals 3, green, calycoid, patent, inner tepals 6, green-yellow, erect, ovate, ca. 4–6 cm long, inside with orange nectaries below the middle; anthers ca. 1.5–2.5 cm long, filaments ca. 1–1.5 cm long; gynoecium yellow-green. Fruits ca. 7 cm long, nutlet samaroid, pale brown, ca. 5 mm long, apex pointed, the nutlets of the lower parts usually persistent.

*Distribution.* Native of northern America (in southern Ontario and the eastern and southeastern United States); cultivated in Kunming, Lushan, Nanjiang, and Qingdao.

*Ecology.* Flowering May; fruiting September–October.

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LIST 1. List of taxa and keys in the order in which they appear in the text. Numbering system corresponds to that in the text.

Magnoliaceae
KEY TO THE GENERA OF MAGNOLIACEAE
MAGNOLIACEAE Subfamily MAGNOLIOIDEAE
Tribe Magnolieae
Tribe Michelieae
Tribe Magnolieae
**I.** Magnolia
KEY TO THE SUBGENERA AND SECTIONS OF MAGNOLIA
KEY TO THE SPECIES OF MAGNOLIA primarily based on floral characters
KEY TO THE SPECIES OF MAGNOLIA primarily based on fruit characters
**a.** Magnolia subg. Magnolia
**1.** Magnolia sect. Gwillimia
KEY TO THE SPECIES OF MAGNOLIA SECTION GWILLIMIA
1. Magnolia albosericea Chun & C. H. Tsoong.
2. Magnolia championii Benth.
3. Magnolia coco (Lour.) DC.
4. Magnolia delavayi Franch.
5. Magnolia henryi Dunn.
6. Magnolia phanerophlebia B. L. Chen

**2.** Magnolia sect. Rytidospermum
KEY TO THE SPECIES OF MAGNOLIA SECTION RYTIDOSPERMUM
7. Magnolia hypoleuca Siebold & Zucc.
8. Magnolia officinalis Rehder & E. H. Wilson.
9. Magnolia rostrata W. W. Smith.

**3.** Magnolia sect. Oyama
KEY TO THE SPECIES OF MAGNOLIA SECTION OYAMA
10. Magnolia globosa Hook, f. & Thomson.
11. Magnolia sieboldii K. Koch.
12. Magnolia sinensis (Rehder & E. H. Wilson) Stapf.
13. Magnolia wilsonii (Finet. & Gagnep.) Rehder.

**4.** Magnolia sect. Gynopodium
KEY TO THE SPECIES OF MAGNOLIA SECTION GYNOPODIUM
14. Magnolia kachirachirai (Kanehira & Yamamoto) Dandy.
15. Magnolia nitida W. W. Smith.

a. Magnolia nitida var. nitida
b. Magnolia nitida var. lotungensis (Chun & C. T. Tsoong) B. L. Chen & Noot., stat. nov.
c. Magnolia nitida var. robusta B. L. Chen & Noot. var. nov.

16. Magnolia omeiensis (Cheng) Dandy.

**5.** Magnolia sect. Alcimandra

17. Magnolia cathcartii (Hook. f. & Thomson) Noot.

**b.** Magnolia subg. Yulania

**1.** Magnolia sect. Yulania

KEY TO THE SPECIES OF MAGNOLIA SECTION YULANIA

18. Magnolia amoena Cheng.
19. Magnolia campbellii Hook. f. & Thomson.
20. Magnolia dawsoniana Rehder & E. H. Wilson.
21. Magnolia heptapeta (Buc'hoz) Dandy.
22. Magnolia sargentiana Rehder & E. H. Wilson.
23. Magnolia sprengeri Pamp.
24. Magnolia zenii Cheng.

**2.** Magnolia sect. Buergeria

KEY TO THE SPECIES OF MAGNOLIA SECTION BUERGERIA

25. Magnolia biondii Pamp.
26. Magnolia cylindrica E. H. Wilson.
27. Magnolia kobus DC.
28. Magnolia stellata (Siebold & Zucc.) Maxim.

**3.** Magnolia sect. Tulipastrum

29. Magnolia quinquepeta (Buc'hoz) Dandy.

**c.** Magnolia subg. Talauma

**1.** sect. Blumiana

30. Magnolia candollii (Blume) H. Keng var. obovata (Korth.)

HYBRIDS AND CULTIVATED SPECIES NOT NATIVE TO CHINA

31. Magnolia xsoulangiana Soulange ex Thieb. sect. Theorodon Spach (of subg. Magnolia)
32. Magnolia grandiflora L.

DUBIOUS SPECIES

**II.** Manglietia

KEY TO THE SPECIES OF MANGLIETIA primarily based on floral characters

KEY TO THE SPECIES OF MANGLIETIA primarily based on fruit characters

**1.** Manglietia Section Manglietia

1. Manglietia aromatica Dandy.
2. Manglietia conifera Dandy.
3. Manglietia dandyi (Gagnep.) Dandy.
4. Manglietia duclouxii Finet & Gagnep.
5. Manglietia fordiana Oliver.
   5a. Manglietia fordiana Oliver var. fordiana
   5b. Manglietia fordiana Oliver var. calcarea (X. H. Song) B. L. Chen & Noot. stat. nov.
   5c. Manglietia fordiana Oliver var. forrestii (W. W. Smith ex Dandy) B. L. Chen & Noot. stat. nov.
   5d. Manglietia fordiana Oliver var. kwangtungensis (Merr.) B. L. Chen & Noot. stat. nov.
6. Manglietia garrettii Craib.
7. Manglietia glauca Blume var. sumatrana (Miq.) Dandy.
8. Manglietia grandis Hu & Cheng.
9. Manglietia hookeri Cubitt & W. W. Smith.
10. Manglietia insignis (Wall.) Blume
11. Manglietia lucida B. L. Chen & S. C. Yang.
12. Manglietia megaphylla Hu & Cheng.
13. Manglietia microtricha Law.
14. Manglietia moto Dandy.
15. Manglietia pachyphylla Chang.
16. Manglietia szechuanica Hu.
17. Manglietia ventii Tiep.

**2.** Section Manglietiastrum

18. Manglietia sinica (Law) B. L. Chen & Noot. comb. nov.

**III.** Kmeria

1. Kmeria septentrionalis Dandy.

Tribe Michelieae

**IV.** Michelia

KEY TO THE SECTIONS OF MICHELIA

KEY TO THE SPECIES OF MICHELIA primarily based on floral characters

KEY TO THE SPECIES OF MICHELIA primarily based on fruit characters

**1.** Michelia Section Michelia

KEY TO THE SPECIES OF SECTION MICHELIA

1. Michelia aenea Dandy.
2. Michelia cavaleriei Finet & Gagnep.
3. Michelia champaca L.
4. Michelia compressa (Maxim.) Sarg.
5. Michelia coriacea Chang & B. L. Chen.
6. Michelia doltsopa Buch.-Ham. ex DC.
7. Michelia elliptilimba B. L. Chen & Noot. sp. nov.
8. Michelia flaviflora Law. & Y. F. Wu.
9. Michelia floribunda Finet & Gagnep.
10. Michelia foveolata Merr. ex Dandy.
11. Michelia fujianensis Q. F. Zheng.
12. Michelia fulva Chang & B. L. Chen.
13. Michelia ingrata B. L. Chen & S. C. Yang.
14. Michelia kisopa Buch.-Ham. ex DC.
15. Michelia lacei W. W. Smith.
16. Michelia macclurei Dandy.
17. Michelia masticata Dandy.
18. Michelia maudiae Dunn.
19. Michelia mediocris Dandy.
20. Michelia microtricha Hand.-Mazz.
21. Michelia shiluensis Chun & Y. Wu.
22. Michelia velutina DC.
23. Michelia wilsonii Finet & Gagnep.
24. Michelia ×alba DC.

**2.** Michelia Section Anisochlamys

25. Michelia hypolampra Dandy.

**3.** Michelia Section Dichlamys

KEY TO THE SPECIES OF SECTION DICHLAMYS

26. Michelia angustioblonga Law.
27. Michelia balansae (A. DC) Dandy.
28. Michelia chapensis Dandy.
29. Michelia leveilleana Dandy.
30. Michelia martinii (H. Lév.) Finet & Gagnep. ex H. Lév.
31. Michelia xanthantha C. Y. Wu ex Law & Y. F. Wu.

**4.** Michelia Section Micheliopsis

32. Michelia figo (Lour.) Sprengel.
    - 32a. Michelia figo var. figo
    - 32b. Michelia figo var. crassipes (Law) B. L. Chen & Noot., stat. nov.
33. Michelia yunnanensis Franchet.

**5.** Michelia Section Tsoongiodendron

34. Michelia odora (Chun) Noot. & B. L. Chen., stat. nov.

**6.** Section Paramichelia

35. Michelia baillonii (Pierre) Finet & Gagnep.

DUBIOUS SPECIES

MAGNOLIACEAE Subfamily LIRIODENDROIDEAE

**V.** Liriodendron

1. Liriodendron chinense (Hemsley) Sarg.
2. Liriodendron tulipifera L.

LIST 2. List of species showing numbering system used in the Collections Examined list that follows.

KMERIA

*1.* K. septentrionalis Dandy
*2.* K. duperreana (Pierre) Dandy

LIRIODENDRON

*3.* L. chinense (Hemsley) Sarg.
*4.* L. tulipifera L.

MANGLIETIA

*5.* M. aromatica Dandy
*6.* M. conifera Dandy
*7.* M. dandyi (Gagnep.) Dandy
*8.* M. duclouxii Finet & Gagnep.
*9.* M. fordiana Oliver var. fordiana
  - *9a.* M. fordiana var. calcarea (X. H. Song) B. L. Chen & Noot.
  - *9b.* M. fordiana var. forrestii (W. W. Smith ex Dandy) B. L. Chen & Noot.
  - *9c.* M. fordiana var. kwangtungensis (Dandy) B. L. Chen & Noot.

*10.* M. garrettii Craib
*11.* M. glauca var. sumatrana (Miq.) Dandy
*12.* M. grandis Hu & Cheng
*13.* M. hookeri Cubitt & W. W. Smith
*14.* M. insignis (Wall.) Blume

*15.* M. lucida B. L. Chen & S. C. Yang
*16.* M. megaphylla Hu & Cheng
*17.* M. microtricha Law
*18.* M. moto Dandy
*19.* M. pachyphylla Chang
*20.* M. sinica (Law) B. L. Chen & Noot.
*21.* M. szechuanica Hu
*22.* M. ventii Tiep

MAGNOLIA

SUBGENUS MAGNOLIA

*Section Gwillimia*

*23.* M. albosericea Chun & C. H. Tsoong
*24.* M. championii Benth.
*25.* M. coco (Lour.) DC.
*26.* M. delavayi Franchet
*27.* M. henryi Dunn
*28.* M. phanerophlebia B. L. Chen

*Section Rytidospermum*

*29.* M. hypoleuca Siebold & Zucc.
*30.* M. officinalis Rehder & E. H. Wilson
*31.* M. rostrata W. W. Smith

*Section Oyama*

*32.* M. globosa Hook. f. & Thomson
*33.* M. sieboldii K. Koch
*34.* M. sinensis (Rehder & E. H. Wilson) Stapf
*35.* M. wilsonii (Finet & Gagnep.) Rehder

*Section Theorhodon*

*36.* M. grandiflora L.

*Section Gynopodium*

*37.* M. kachirachirai (Kanehira & Yamamoto) Dandy
*38.* M. nitida W. W. Smith var. nitida
*38a.* M. nitida var. lotungensis (Chun & C. T. Tsoong) B. L. Chen & Noot.
*38b.* M. nitida var. robusta B. L. Chen & Noot.
*39.* M. omeiensis (Cheng) Dandy

*Section Alcimandra*

*40.* M. cathcartii (Hook. f. & Thomson) Noot.

SUBGENUS YULANIA

*Section Yulania*

*41.* M. amoena Cheng
*42.* M. campbellii Hook. f. & Thomson
*43.* M. dawsoniana Rehder & E. H. Wilson
*44.* M. heptapeta (Buc'hoz) Dandy
*45.* M. sargentiana Rehder & E. H. Wilson
*46.* M. sprengeri Pamp.
*47.* M. zenii Cheng

*Section Buergeria*

*48.* M. biondii Pamp.
*49.* M. cylindrica E. H. Wilson
*50.* M. praecocissima Koidz.
*51.* M. tomentosa Thunb.

*Section Tulipastrum*

*52.* M. quinquepeta (Buc'hoz) Dandy
*53.* M. ×soulangiana Soulange ex Thieb.

SUBGENUS TALAUMA

*Section Blumiana*

*54.* M. candollii var. obovata (Korth.) Noot.

MICHELIA

*Section Michelia*

*55.* M. ×alba DC.
*56.* M. champaca L.
*57.* M. doltsopa Buch.-Ham. ex DC.
*58.* M. elliptilimba B. L. Chen & Noot.
*59.* M. flaviflora Law & Y. F. Wu
*60.* M. floribunda Finet & Gagnep.
*61.* M. fulva Chang & B. L. Chen
*62.* M. kisopa Buch.-Ham. ex DC.
*63.* M. microtricha Hand.-Mazz.
*64.* M. velutina DC.
*65.* M. wilsonii Finet & Gagnep.
*66.* M. aenea Dandy
*67.* M. cavaleriei Finet & Gagnep.
*68.* M. compressa (Maxim.) Sarg.
*69.* M. coriacea Chang & B. L. Chen
*70.* M. foveolata Merr. ex Dandy
*71.* M. fujianensis Q. F. Zheng
*72.* M. ingrata B. L. Chen & S. C. Yang
*73.* M. lacei W. W. Smith
*74.* M. macclurei Dandy
*75.* M. masticata Dandy
*76.* M. maudiae Dunn
*77.* M. mediocris Dandy
*78.* M. shiluensis Chun & Y. Wu

*Section Anisochlamys*

*79.* M. hypolampra Dandy

*Section Dichlamys*

*80.* M. angustioblonga Law & Y. F. Wu
*81.* M. balansae (A. DC) Dandy
*82.* M. chapensis Dandy
*83.* M. leveilleana Dandy
*84.* M. martinii (H. Lév.) Finet & Gagnep. ex H. Lév.
*85.* M. xanthantha C. Y. Wu ex Law & Y. F. Wu

*Section Micheliopsis*

*86.* M. figo (Lour.) Sprengel var. figo
*86a.* M. figo var. crassipes (Law) B. L. Chen & Noot.
*87.* M. yunnanensis Franchet ex Finet & Gagnep.

*Section Tsoongiodendron*

*88.* M. odora (Chun) Noot. & B. L. Chen

*Section Paramichelia*

*89.* M. baillonii (Pierre) Finet & Gagnep.

LIST 3. List of exsiccatae. Numbers in italics following the colon after the collection number refer to species numbered as in List 2. [Please note: herbarium designations are not given because this part of the first author's

notes remains in China and has not yet been made available. The history of the project is outlined in the introductory section to the article.]

*An Shun Exped. 1112*: *35*; *Anderson T. 5*: *57*; *Ao H.X. 8117*: *67*.

*Badal Khan 102*: *89* (type); *Balansa B. 3884*: *24* (type), *3885*: *24* (type), *3886*: *81* (type), *3887*: *6* (type), *3889*: *6* (type), *4580*: *55*; *Barrett G. s.n.*: *9*; *Bartholomew and Boufford 3862*: *42*; *Beauvais 321*: *25*; *Beiliu Yizu 8 4102*: *6*; *Bernardi 19891*: *68*; *Bock C. et A. v. Rosthorn 2325*: *65*; *Bodinier E. & Ducloux 47*: *44*, *& Ducloux 116*: *87* (type), *& Ducloux 168*: *87*, *1211*: *9*, *1221*: *24*; *Bon M. l'abbé 3176*: *24* (type); *Bonnet A. s.n.*: *7*; *Bons d'Anty 30*: *87*; *Brillet 16*: *6*; *Buerger s.n.*: *51* (type).

*Cai C.X. 77-2*: *67*, *5142 14-V*: *38*, *5143*: *38*, *5465 29-V*: *24*, *5470*: *38a*; *Calléry 153*: *56*; *Cao T.M. 830703*: *14*; *Cao Zi-yu 369*: *33*; *Carles s.n.*: *52*: *44*, *4*: *44*; *Cavalerie J. & E. Bodinier s 0*: *30*, *s.n.*: *67*, *1562*: *84*, *2263*: *9a*, *& Fortunat 2263*: *67* (type), *3044*: *14*, *3045*: *67* (type), *3045 A*: *67* (type), *3182*: *9a*, *4619*: *87*, *7111*: *52*, *7150*: *44*, *7312*: *67*, *7313*: *50*, *7315*: *52*, *7402*: *44*, *7777*: *44*, *7800*: *44*; *Cave G.H. s.n.*: *32*; *C.C.C.* (*Levine*) *1558*: *76*, (*To Kang Peng cs*) *12179*: *7* (type), *12344*: *9c* (type), *13292*: *74*, (*McClure*) *14599*: *70*; *Champion 37*: *24* (type), *37*: *24* (type); *Chan K.Y. 1033*: *9*; *Chan Shi Sam 5236*: *55*; *Chan Y.P. 355*: *26*, *360*: *26*; *Chang C.C. 11316*: *77*, *11432*: *5*, *11438*: *16*, *12292*: *70*, *13670*: *82*; *Chang C.E. 3289*: *68*, *3651*: *68*, *4384*: *37*, *8825*: *68*; *Chang H.T. 1564*: *73*, *3375*: *86*, *4029*: *52*, *4620*: *44*, *4621*: *14*, *4700*: *67* (type), *5022*: *38*, *5062*: *87*, *5094*: *3*, *5129*: *87*, *5215*: *52*, *5218*: *3*, *5244*: *49*, *5309*: *3*, *5394*: *3*, *5396*: *3*, *5659*: *65*, *5702*: *84*, *5747*: *87*, *5824*: *87*, *6037*: *86a*, *6081*: *81*, *6095*: *9*, *6268*: *87*, *6342*: *7*, *6477*: *87*, *6663*: *11*, *6824*: *79*, *6825*: *79*, *7044*: *86*, *7471*: *76*, *7472*: *76*, *7474*: *76*, *86031*: *24*, *86094*: *24*, *860088*: *9*; *Chang Panti 81390*: *65*; *Chang Q.L. 12055*: *65*; *Chang W.X. 8403*: *33*; *Chehkiang 190*: *86*; *Chen B.L.* (*the order is that of the last number*) *86 G 1*: *82*, *87 T 1*: *28*, *B 0 1*: *42*, *& C.N. Mai 87 T 2*: *15*, *B 0 2*: *49*, *86 S 0 3*: *67*, *87 T 3*: *28*, *B 0 3*: *49*, *86 G 4*: *6*, *B 0 4*: *42*, *GS 9 5*: *16*, *B 0 5*: *42*, *86 G 6*: *77*, *GS 9 6*: *16*, *B 0 6*: *42*, *86 G 7*: *24*, *B 0 7*: *43*, *B 0 8*: *30*, *87 T 11*: *82* (type), *87 T 0 13*: *57*, *87 T 14*: *38*, *& C.N. Mai 87 T 19*: *72* (type), *87 T 20*: *5*, *87 T 21*: *38*, *87 T 22*: *5*, *87 T 23*: *26*, *Gs 9 25*: *20*, *87 T 29*: *57*, *87 T 30*: *57*, *87 T 31*: *38*, *87 T 32*: *13*, *87 T 33*: *82* (type), *87 T 34*: *81*, *86 S 49*: *57*, *86 S 0 50*: *57*, *86 S 51*: *73*, *& Su 86 S 53*: *14* (type), *87 T 61*: *14*, *87 T 62*: *60*, *87 T 63*: *40*, *87 T 65*: *64*, *87 T 82*: *38*, *87 T 99*: *8*, *87 F 105*; *7*, *87 T 106*: *9b*, *87 T 107*: *60*, *87 T 108*: *82*, *135*: *9*, *87 Gz 149*: *23*, *150*: *7*, *87 Gz 150*: *9*, *87 GZ 151*: *11*, *87 GZ 152*: *6*, *87 K 157*: *87*, *87 G 161*: *7*, *87 G 162*: *86*, *87 F 164*: *26*, *87 F 165*: *56*, *F 166*: *52*, *87 F 167*: *57*, *87 F 168*: *72*, *87 F 169*: *1*, *87 F 171 6-X-*: *15*, *87 F 173*: *1*, *87 F 177*: *69*, *86 GS 177*: *14*, *86 GS 177*: *14*, *87 F 178*: *69* (type), *87 F 180*: *20*, *87 F 181 10-X*: *16*, *87 F 182*: *7*, *87 F 183*: *64*, *87 F 184*: *7*, *87 F 185*: *6*, *86 S 186*: *14*, *86 S 187*: *14*, *87 F 187*: *14*, *86 S 190*: *14*, *86 S 192*: *82*, *87 F 192*: *6*, *86 S 193*: *66* (type), *GL 86-193*: *61* (type), *87 F 194*: *6*, *87 F 195*: *6*, *87 F 196*: *24*, *87 F 197*: gb, *87 F 198*: *8*, *887 F 200*: *60*, *87 F 201*: *7*, *87 F 203*: *38*, *87 F 205*: *16*, *87 F 206*: *16*, *87 F 219*: *7*, *87 F 220*: *8*, *87 F 221*: *7*, *87 F 222*: *24*, *87 F 223*: *81*, *87 F 224*: *60*, *87 F 225*: *60*, *87 F 226*: *14*, *77 F 227*: *26*, *87 F 228*: *87*, *87 F 253*: *82*, *86 S 256*: *14*, *86 S 297*: *12*, *86 S 299*: *12*, *GS 302*: *66*, *315*: *9*, *370*: *7*, *86 S 478*: *14*, *86 S 479*: *60*, *86 S 485*: *14*, *86 S 486*: *5*, *86 S 487*: *6*, *86 S 468*: *14*, *86 S 507*: *24*, *86 S 510*: *24*, *86 S 517*: *38*, *86 S 533*: *82* (type), *86 S 538*: *24*, *86 S 539*: *72*, *87 G 2151*: *11*, *87 G 2154*: *77*, *87 G 2155*: *78*, *GS 3240*: *38*, *GS 8676*: *40*, *GS 8698*: *6*, *GS 9023*: *38*, *GS 9028*: *60*, *GS 9035*: *69* (type), *GS 9044*: *57*, *GS 9047*: *72*, *80109*: *9*, *80110*: *76*, *80115*: *7*, *et al. 81001*: *30*, *81006*: *86a*, *81007*: *86a*, *81008*: *70*, *GS 86002*: *66*, *GS 86075*: *60*, *GS 86100*: *82*, *GS 86102*: *73* (type), *GS 86103*: *14*, *GS 86177*: *14*, *GS 86178*: *12*, *GS 86179*: *12*, *GS 86180*: *12*, *GS 86182*: *6* (type), *GS 86184*: *14*, *GS 86186*: *14*, *GS 86187*: *66*, *GS 86188*: *60*, *GS 86189*: *66*, *GS 86191*: *12*, *GS 86194*: *15*, *GS 86195*: *15*, *GS 86237*: *57* (type), *GS 86238*: *26*, *GS 86239*: *57*, *Gs 86243*: *5*, *87157*: *26*, *GS 863348*: *7*; *Chen C. 452*: *14*; *Chen H.C. 1675*: *86*, *500224*: *6*; *Chen J.C. 745*: *3*; *Chen L.C. 500183*: *7*; *Chen M. 1321*: *49*, *3792*: *60*; *Chen M.L. 3-5535*: *24*; *Chen Q.H. 942*: *6*; *Chen S. 587*: *30*, *1190*: *30*, *1315*: *86*, *1736*: *44*, *1899*: *44*, *2692*: *41* (type), *2706*: *44*, *2775*: *76*, *2828*: *76*; *Chen S.J. et al. 840055*: *52*, *840092*: *14*; *Chen S.P.*; *1131*: *74*; *Chen T.C. 617*: *9c*, *707*: *82*; *Chen Y.F. 1657*: *68*; *Chen Y.L. 192*: *44*; *Chen Y.W. 7620*: *38a*; *Chen Z.Z. 50986*: *14*, *51010*: *67*, *51134*: *14*, *51153*: *14*, *51165*: *33*, *51353*: *3*, *51516*: *86*, *51808*: *70*, *51881*: *67*, *52125*: *14*, *52375*: *82*, *52523*: *3*, *52664*: *67*, *52980*: *76*; *Cheng Fung Tung CCC*, *s.n.*: *86*; *Cheng W.C. & C.T. Hwa 688*: *60*, *889*: *83*, *938*: *83*, *1005*: *60* (type), *1049*: *46*, *1066*: *44*, *1160*: *30*, *1171*: *52* (type); *Cheng W.C. 4030*: *9*, *4233*: *47* (type), *4444 A*: *41* (type), *10525*: *39* (type); *Cheo & Wilson 12746*: *44*; *Chevalier A. 29374*: *4*, *30103*: *81*, *30744*: *82* (type), *37032*: *14*, *37339*: *6*, *37877*: *7*, *37880*: *24*, *38185*: *79*, *38404*: *14*, *38537*: *6*, *168*: *65*, *& C.S. Fan 168*: *65*, *& C.S. Fan 436*: *30*, *& C.S. Fan 444*: *52*, *1230*: *25*, *1234*: *52*, *1255*: *52*, *1864*: *3*, *2064*: *51*, *2069*: *44*, *2099*: *65*, *2560*: *3*, *2582*: *44*, *2597*: *29*, *2825*: *44*, *& E.D. Merrill 14042*: *36*, *field nr 1050 14349*: *30*, *herb. no. 14884*: *52*, *herb. nr. 18560*: *3*, *18603*: *44*, *18702*: *44*, *18759*: *30*, *herb. nr. 18844*: *3*; *Chien S.S. 5889*: *44*; *Chin T.H. 8218*: *6*; *Ching I Peng 3446*: *68*; *Ching R.C. 1602*: *44*, *1610*: *30*, *1904*: *25*, *1986*: *86*, *2037*: *52*, *2066*: *76*, *2167*: *38a*, *2211*: *86*, *2370*: *3*, *2403*: *44*, *2452*: *76* (type), *2472*: *9*, *2501*: *49*, *2519*: *30*, *2617*: *44*, *2865*: *44*, *2946*: *9*, *2949*: *49* (type), *2975*: *33*, *2979*: *33*, *2994*: *49* (type), *3035*: *33*, *3227*: *30*, *4764*: *44*, *5119*: *52* (type), *5247*: *1* (type), *5613*: *86*, *5625*: *86*, *5910*: *9b*, *6075*: *14*, *7091*: *44*, *7117*: *6* (type), *7421*: *5* (type), *7549*: *55*, *7949*: *24*, *8144*: *81*, *8329*: *70*, *8390*: *6* (type), *8394*: *9*, *20455*: *26*, *20523*: *42*, *21364*: *86*, *21586*: *42*, *21681*: *46*, *22016*: *32*; *Chiu P.Y. 7743*: *3*; *Chow H.C. 46*: *30*, *334*: *46*, *484*: *14* (type), *896*: *52*, *1076*: *14*, *1094*: *3*, *1367*: *30*, *8255*: *84*, *8258*: *84*, *8638*: *52*, *9777*: *45*, *11944*: *21*; *Chow H.C. 12095*: *39*; *Chow K.S. 126*: *30*, *145*: *86*; *Chu K.L. 2505 a*: *29*, *3908*: *45*; *Chuang C.C. 2442*: *68*; *Chuk Tsz Haang 13775*: *86*; *Chun N.K. 40574*: *86*, *41303*: *86*, *42500*: *76*, *& C.L. Tso 43417*: *24*, *& C.L. Tso 43687*: *9*, *& C.L. Tso 43749*: *81*, *& C.L.*

*Tso 43956*: *9*, *& C.L. Tso 44041*: *38a*, *& C.L. Tso 44042*: *38a*, *& C.L. Tso 44233*: *70*, *& C.L. Tso 44257*: *88* (type); *Chun S.H. 4466*: *74*, *9729*: *6*, *10035*: *9*, *10140*: *7*, *12003*: *24*, *12578*: *24*, *14206*: *6*, *15258*: *67*, *15509*: *38*, *15634*: *86*, *15857*: *14*, *15907*: *76*, *94617*: *67*; *Chun W.Y. 69*: *44*, *119*: *55*, *136*: *56*, *4409*: *48*, *4520*: *25*, *5856*: *86*, *5860*: *7*, *5933*: *70*, *5963*: *76*, *6481*: *24*, *6481 A*: *25*, *6511*: *55*, *7179*: *70*, *7353*: *18*; *Chun Y.F. 30423*: *76*; *Chun Y.F. 81654*: *33*; *Chung H.H. 213*: *3*, *& S.C. Sun 392*: *44*, *& S.C. Sun 680*: *30*, *740*: *55*, *742*: *86*, *779*: *25*, *1276*: *86*, *1620*: *86*, *2288*: *86*, *2423*: *86*, *2452*: *36*, *2454*: *55*, *2495*: *36*, *2496*: *55*, *2510*: *25*, *2823*: *86*, *2833*: *86*, *2940*: *9*, *3374*: *86*, *3667*: *76*, *3670*: *86*, *5921*: *86*, *6020*: *36*, *6280*: *86*, *6815*: *86*, *6903*: *86*, *8492*: *25*; *Clemens J. & M.S. 4281*: *70*; *Cribb P.J. c 84*: *9*; *Cubitt G.E.S. 20*: *13* (type).

*Da Yao Shan Exped. 10240*: *38a*, *10756*: *60*, *10952*: *77*, *11080*: *70*, *11180*: *82*, *13429*: *38a*; *Dalziel (herbarium) s.n.*: *55*, *s.n.*: *86*; *Dang C.Z. 886*: *87*, *1618*: *70*, *1656*: *65*; *David M. l'Abbé s.n.*: *45* (type), *s.n.*: *45* (type), *s.n.*: *45*; *Delavay s.n.*: *87*, *s.n.*: *46*, *168*: *87*, *2231*: *26* (type), *4218*: *87*, *4884*: *87* (type), *6616*: *87*, *6786*: *87*, *6818*: *8* (type), *6828*: *8*; *Deng C.Y. 84130*: *84*; *Deng X.F. 129*: *52*, *201*: *67*, *231*: *38a*, *10634*: *24*; *Deng & Yao 79147*: *3*, *79192*: *33*; *Dian Dongbei Exped. 754*: *83* (type); *Ding C.S. T 575*: *41*; *Donnat 38118*: *6*, *38191*: *81*; *Du D.H. 3354*: *67*, *3854*: *67*; *Ducloux F. 93*: *87*, *& Bodinier 116*: *87*, *635*: *87*, *2133*: *8* (type), *2393*: *30*, *2848*: *26*, *3794*: *87*, *6932*: *35*; *Dunn 2448*: *86* (type).

*Eberhardt 2705*: *24*; *Esquirol 3061*: *25*, *4046*: *87*, *5104*: *87*, *6346*: *87*.

*Fan C.S. & Y.Y. Li 191*: *44*, *261*: *44* (type), *281*: *30*; *Fang W.P. 2343*: *52*, *12018*: *44*, *12275*: *44*, *13256*: *52*, *15738*: *84*, *15969*: *65*, *16598*: *65*, *16951*: *21*, *18950*: *21*; *Farges R.P. s.n.*: *84*, *s.n.*: *46*, *70*: *30*, *94*: *46*, *219*: *46*, *702*: *4*, *771*: *30*, *1300*: *48* (type), *1324*: *84*, *1394*: *84* (type), *1447*: *52*; *Faurie U. 536*: *33*, *537*: *33*, *3372*: *29*, *42556*: *29*, *6300*: *29*; *Feng K.M. 4813*: *32*, *4824*: *57*, *5193*: *9b*, *11069*: *14*, *11169*: *26*, *11302*: *14*, *11447*: *3* (type), *11558*: *3* (type), *11771*: *7*, *11808*: *16*, *11990*: *5*, *12030*: *69* (type), *12254*: *9b*, *12392*: *9b*, *12464*: *69*, *12636*: *87*, *12691*: *14*, *12844*: *72*, *12895*: *12*, *12933*: *14*, *13009*: *5*, *13191*: *72*, *13274*: *84*, *13276*: *72*, *13599*: *81*, *13713*: *14*, *13722*: *7*, *13743*: *60*, *13951*: *14*, *13960*: *7*, *13973*: *82*, *14025*: *70*, *14117*: *60*, *21124*: *42*, *22207*: *14*, *22369*: *8*, *22416*: *40*, *22710*: *27*, *22778*: *7*, *72059*: *23*; *Fenzel G. 2893*: *48*, *2951*: *48*; *Fleury F. 30103*: *81*, *30158*: *79* (type), *37667*: *79*, *in Chevalier 37945*: *7*; *Forbes F.B. s.n.*: *44*, *2202*: *44*; *Ford C. 90*: *9* (type), *22224*: *9*; *Forrest G. 57*: *26*, *140*: *42* (type), *482*: *87*, *2104*: *87*, *2174*: *52*, *4105*: *60*, *5539*: *52*, *6105*: *26*, *7182*: *35* (type), *7725*: *13*, *7964*: *26*, *8459*: *52*, *8678*: *14*, *8948*: *57*, *8949*: *57*, *9119*: *57*, *9320*: *60*, *9460*: *60*, *9588*: *60*, *9860*: *57*, *9907*: *14*, *10580*: *26*, *11652*: *26*, *11811*: *13*, *11848*: *14*, *11860*: *42*, *11913*: *57*, *11988*: *9b*, *12089*: *57*, *12221*: *44*, *12282*: *87*, *12915 bis*: *42*, *13253*: *42*, *13513*: *35*, *14188*: *14* (type), *14248*: *42*, *14402*: *14*, *14466*: *42* (type), *14868*: *42*, *14945*: *14*, *15052*: *42*, *15056*: *14*, *15059*: *38* (type), *15480*: *57*, *15496*: *35*, *15505*: *26*, *15780*: *57*, *15892*: *26*, *15952*: *13*, *16090*: *60*, *16388*: *42*, *16403*: *42*, *17188*: *14*, *17248*: *42*, *17300*: *38*, *17301*: *42* (type), *17654*: *57*, *17809*: *57*, *17868*: *42*, *17955*: *14*, *18083*: *42* (type), *18246*: *31* (type), *18341*: *14*, *18371*: *14*, *18494*: *57*, *18497*: *57*, *18512*: *32* (type), *18600*: *14*, *18780*: *57*, *18790*: *42* (type), *18870*: *32* (type), *18930*: *42*, *18959*: *32*, *18964*: *14*, *19985*: *31*, *20050*: *32*, *20080*: *14*, *20303*: *32*, *20309*: *42*, *20358*: *38* (type), *20711*: *44*, *20827*: *31*, *20841*: *42*, *20844*: *14*, *20860*: *38*, *20866*: *32*, *21080*: *60*, *21515*: *44*, *21615*: *42*, *21616*: *38*, *21644*: *31* (type), *21722*: *32*, *22841*: *42*, *22869*: *38*, *22926*: *32*, *23480*: *35*, *23481*: *35*, *24012*: *57*, *24050*: *57*, *24118*: *42*, *24207*: *14*, *24214*: *42*, *24217*: *57*, *24255*: *42*, *24351*: *42*, *24419*: *56*, *24700*: *52*, *25167*: *57*, *25200*: *14*, *25208*: *60*, *25287*: *42*, *25288*: *42*, *25302*: *56*, *25319*: *60*, *25655*: *42*, *25751*: *31*, *26198*: *60*, *26239*: *60*, *26258*: *57*, *26286*: *42*, *26293*: *42*, *26310*: *14*, *26381*: *38* (type), *26383*: *57*, *26393*: *42*, *26509*: *38*, *26580*: *57*, *26639*: *13*, *26685*: *14*, *26689*: *14*, *26694*: *9b*, *26705 A*: *9b* (type), *26726*: *14*, *26736*: *14*, *26738*: *14*, *27299*: *14*, *27300*: *9b*, *27363*: *60* (type), *27364*: *13*, *27365*: *14*, *27379*: *57*, *27680*: *60*, *27707*: *57*, *27710*: *57*, *27711*: *31*, *27735*: *38*, *27941*: *35*, *27979*: *26*, *29093*: *42*, *29129*: *35*, *29354*: *60*, *29411*: *57*, *29620*: *14*, *29747*: *13*, *29770*: *60*, *29780*: *56*, *29821*: *31*, *29962*: *52*, *30385*: *38*, *30386*: *42*, *30391*: *31*, *30962*: *26*, *31002*: *35*; *Fu G.A. 1713*: *70*; *Fu J.R. 187*: *86*; *Fu K.T. 2457*: *44*, *2880*: *44*; *Fung Hom 2-30*: *44*, *2-72*: *44*, *10833*: *70* (type), *11064*: *70*, *18635*: *44*, (*Lingn Un. Herb.*) *18678*: *44*, (*Lingn. Un. Herb.*) *18763*: *25*, *20057*: *24*, *21360*: *55*; *Funkhouser W.L. C.C.C. 9082 a*: *9*; *Furuse, Miyoshi 1883*: *68*, *3763*: *68*.

*Gao C.Z. 42288*: *6*; *Gao T.X. et al. 1*: *5*, *et al. 4*: *70*, *5*: *7*; *Gao Z.Y. 126*: *47*; *Garrett H.B.G. 114*: *10* (type); *Gaudichaud Voy. sur la Bon 228*: *25*, *232*: *25*; *Ghof & Tsoong 1961*: *6*; *Giraldi Los. 1897*: *48*; *Gongda 1547*: *82*, *740250*: *60*; *Griffith 68 B*: *64*, *71*: *57*; *Groff G.W. s.n.*: *86*, *s.n.*: *44*, (*CCC herb. nr.*) *11717*: *44*; *Guan Z.T. 8263*: *60*; *Guang 168*: *76*, *225*: *70*, *242*: *19*; *Guangdong Mucai Yanjiu Zu 32*: *38a*; *Guangfu Exped. 19*: *67*, *463*: *6*, *465*: *6*, *877*: *67*, *1031*: *76*; *Guileier 40937*: *81*; *Gulin Yiyao Gongsi 846*: *8*; *Guo Y.Q. 8463*: *57*.

*HFSI 38315*: *81*, *88315*: *81*, *88323*: *9*, *88355*: *9*, *88356*: *77*, *88383*: *81*, *88564*: *77*, *88605*: *9*, *88727 a*: *77*, *88730*: *81*; *Hainan Exped. 752*: *70*; *Hainan Gong Zuo Zhan 643*: *24*, *1019*: *81*, *1701*: *24*; *Hainan Zu 75 265*: *56*; *Hand.-Mazz. 6*: *87*, *294*: *86*, *683*: *67*, *1552*: *14*, *2099*: *14*, *2204*: *14*, *2495*: *14*, *4863*: *26*, *8304*: *42*, *9126*: *31* (type), *9188*: *42*, *9212*: *32*, *9853*: *42*, *10012*: *42*, *10672*: *14*, *& T.H. Wang 11131*: *14*, *& Wang Te Hui 12281*: *67* (type); *Hara c.s. 630283 3*: *64*, *630691 9*: *42*; *He J.D. 5040*: *82*; *He S.C. 85170*: *67*; *Henry A. 163*: *86*, *548*: *46*, *549*: *30*, *956*: *68*, *1261*: *68*, *1467*: *68* (type), *1467 A*: *68*, *1475*: *30*, *1543*: *68*, *1836*: *4*, *1836 A*: *4*, *1984*: *68*, *2060*: *37*, *2522*: *46*, *3711*: *30*, *4886*: *30*, *5389*: *30* (type), *5389 a*: *30* (type), *5651*: *46*, *5836*: *3*, *6597*: *46*, *6597 A*: *46*, *7733*: *48*, *9429*: *87*, *9429 a*: *87*, *9450*: *26*, *9450 A*: *26*, *9545*: *89*, *10892*: *60*, *11441*: *84*, *11572*: *60*, *11572 B*: *60*, *11572C*: *60*, *11572 D*: *60*, *11988*: *9b*, *12782 A*: *27* (type), *13147*: *55*, *13277*: *87*, *13421*: *89*, *13513*: *89*; *Hers J 457*: *48*, *541*: *48*, *622*: *44*, *991*: *48*, *1159*: *46*, *1343*: *48*; *Ho H.T. 60175*: *76*; *Ho Y.Y. 2364*: *49*, *2485*: *33*, *3200*: *76*, *3201*: *30*; *Hongkong Herbarium No. 1421*: *86*, *2065*: *76* (type), (*Dunns expedit.*) *2325*: *76*, *2326*: *86*, *2448*: *86*

(type); *Hooker J.D. s.n.*: *40* (type), *s.n.*: *42* (type), *s.n.*: *32* (type), *s.n.*: *57*, *s.n.*: *64*, *s.n.*: *40* (type), *s.n.*: *42* (type), *s.n.*: *32* (type), *s.n.*: *54* (type), *15*: *29*; *Hook.f. & Thomson s.n.*: *100* (type), *997*: *64*, *26393*: *42*; *Hosseus C.C. 480*: *56*; *Hotta M. s.n.*: *68*; *How F.C. & N.K. Chun 70147*: *81*, *70468*: *24*, *70732*: *9*, *70963*: *24*, *71674*: *9*, *71797*: *24*, *71849*: *24*, *72059*: *23*, *72157*: *9*, *72342*: *81*, *72569*: *24*, *72740*: *23* (type), *73194*: *74*, *73242*: *81*, *73257*: *81*, *73395*: *9*, *73444*: *9*, *73480*: *81*, *73631*: *78*; *Hsia W.Y. s.n. 7-X-*: *44*; *Hsieh A-tsai s.n.*: *55*; *Hsiung Y.K. 6307*: *86*; *Hsu C.C. & M.T. Kao K 3680*: *68*; *Hu H.H. 93*: *30*, *190*: *86*, *1256*: *86*, *1410*: *3*, *9592*: *3*, *67125*: *32*; *Hu S.Y. 5329*: *36*, *5364*: *86*, *5393*: *25*, *5485*: *55*, *6550*: *86*, *7287*: *9*, *7664*: *9*, *9125*: *9*, *10169 A*: *9*, *10194*: *25*, *10201*: *25*, *10504*: *55*, *10610*: *24*, *11578*: *86*, *12025*: *24*, *12578*: *9*, *12946*: *53*, *13540*: *86*, *13568*: *82*; *Hu W.K. 8809*: *84*, *8879*: *84*, *9211*: *84*; *Huan Jiang Exped. 4-3-1459*: *24*; *Huang D.A. 6034*: *30*, *60393*: *6*; *Huang D.F. 614*: *6*, *1623*: *3*, *1651*: *5*; *Huang D.S. 2 219*: *6*; *Huang D.Z. 3883*: *79*; *Huang S.L. 8018*: *67*, *200001 4*: *86*; *Huang T.C. & M.T. Kao 5127*: *68*, *c.s. 10623*: *68*; *Huang Z.F. 20*: *67*; *Huang Z.H. 66966*: *6*; *Huangshan Exped. 3049*: *19*; *Hunan Exped. 387*; *14*; *Hwa C.T. 38*: *30*, *65*: *48*, *81*: *52*, *104*: *48*, *213*: *44*, *213*: *46*, *276*: *52*, *317*: *60*, *357*: *83*, *381*: *65*, *404*: *30*, *441*: *84*, *502*: *65*, *503*: *60*, *528*: *46*.

*Idzumi M. s.n.*: *29*; *Inokuma T. s.n.*: *50*; *Ip Yuk Shing 817*: *77*.

*Jian Z.P. 50796*: *33*; *Jiang R.B. 13*: *67*; *Jinxiu 15149*: *70*, *20202*: *76*, *20230*: *7*.

*KUN 345*: *89*, *76298*: *8*; *Kanai H. 6120*: *33*, *731152*: *50*; *Kang Ping CCC 15*: *86*; *Kawakami T. 29*: *68*; *Kellogg J. s.n. 2-IX*: *53*; *Keng H. s.n.*: *68*, *K 1048*: *68*; *Keng Y.L. 309*: *30*, *452*: *44* (type), *453*: *44*; *Kerr A.F.G. 4679*: *60* (type), *21027*: *60*; *Kingdon Ward F. 58*: *60*, *331*: *57*, *370*: *38*, *529*: *31*, *3152*: *42*, *3709*: *14*, *5497*: *57*, *9374*: *57*, *10182*: *100*, *10365*: *42*, *10418*: *42*, *10461*: *32*, *10973*: *32*, *10980*: *64*, *17611*: *42*, *19211*: *57*, *19299*: *57*, *20123*: *64*, *20885*: *31*; *Kit Yock Chan 1352*: *25*; *Ko S.P. 50101*: *86*, *50379*: *82*, *50392*: *86*, *50410*: *70*, *50520*: *76*, *50540*: *24*, *50777*: *82*, *50884*: *76*, *51082*: *76*, *51109*: *88*, *51110*: *76*, *51152*: *70*, *51733*: *74*, *51777*: *6*, *51928*: *88*, *52175*: *24*, *52231*: *24*, *52263*: *9*, *52273*: *9*, *52279*: *81* (type), *52664*: *76*, *52807*: *44*, *52870*: *76*, *52921*: *6*, *53079*: *44*, *53301*: *76*, *53514*: *18*, *53609*: *9*, *53691*: *38a*, *53697*: *38q* (type), *53762*: *84*, *53912*: *76*, *54036*: *76* (type), *54122*: *84*, *54186*: *70* (type), *54298*: *9*, *54522*: *70*, *55702*: *81*, *55785*: *70*, *80256*: *76*, *80358*: *84* (type); *Kunming Gongzuozhang 382*: *89*; *Kuo C.M. 8956*: *55*; *Kwok S.P. 80166*: *67*, *80205*: *76*, *80335*: *70*.

*Lace J.H. 5928*: *73* (type); *Lamont J. 53089*: *44*; *Lau S.K. 50*: *81*, *930*: *86*, *1560*: *24*, *2142*: *86*, *2552*: *76*, *3545*: *24*, *4047*: *86*, *4246*: *9* (type), *4348*: *86*, *4850*: *9*, *4854*: *76*, *5245*: *77*, *25954*: *70*, *25956*: *9*, *26532*: *24*, *26589*: *70*, *26947*: *24*, *26969*: *81*, *26975*: *9*, *27375*: *38a*, *27946*: *81*, *28274*: *81*, *28744*: *6*; *Law Y.W. 306*: *60*, *1385*: *44*, *4074*: *5*, *6051*: *78*, *6067*: *27*, *7032*: *14*, *7033*: *14*, *7066*: *70* (type), *7071*: *87*; *Lee S.K. 200723*: *74*; *Lee T.C. 4506*: *84*; *Legendre 863*: *35*, *1704*: *87*; *Leveillé H. 3044*: *14*; *Levine C.O. CCC 920*: *55*, *1345*: *9*, *& McClure 6389*: *86*; *Li Bo Exped. 1170*: *24*; *Li B.G. et al. 59*; *38a*; *Li H.Q. 40046*: *82*; *Li M.K. 3*: *75* (type), *59*: *64* (type), *1729*: *57*, *2329*: *32*, *3515*: *13*, *34500*: *13*; *Li Sheng-tang & Su Yu-Zhen 81 73*: *87*; *Li S.P. Mu 199*: *9b*; *Li T.Z. 1458*: *24*; *Li W.F. 60700*: *65*; *Li W.Z. 8271*: *13*; *Li Y.H. 2066*: *89*, *3607*: *27*, *4068*: *13*, *4262*: *79*, *5789*: *63*, *401415*: *6*; *Li Y.K. 185*: *24*, *430*: *8*, *591*: *67*, *8879*: *83*, *8921*: *46*, *11284*: *84*, *401535*: *9*, *401573*: *82*, *402692*: *77*; *Li Zhen-yu et al. 1899*: *67*; *Li Z.J. 653*: *86*, *1636*: *24*, *3071*: *5*; *Li Z.Q. 99*: *70*; *Li Z.T. 1708*: *67*, *602441*: *70*, *603835*: *7*, *604032*: *70*; *Li Z.Y. 56*: *14*; *Li Z.Z. 822042 3*: *65*; *Liang C.F. 30247*: *6*, *30248*: *38*, *30350*: *6*, *30360*: *6*, *31067*: *67*, *31751*: *70*, *31845*: *74*, *33243*: *25*, *34193*: *11*, *34214*: *81*; *Liang C.X. 77-15*: *84*; *Liang H.Y. s.n. 14-V*: *24*, *60564*: *70*, *60733*: *24*, *61068*: *70*, *61340*: *77*, *61546*: *77*, *61617*: *9*, *61644*: *24*, *61649*: *24*, *62603*: *9*, *63698*: *24*, *64334*: *24*, *64451*: *9*, *64452*: *9*, *64632*: *24*, *64633*: *24*, *64908*: *81*, *64988*: *24*, *65255*: *9*, *67370*: *70*, *69538*: *6*, *69622*: *24*, *69747*: *81*, *100218*: *30*; *Liang J.Y. 100311*: *82*, *100312*: *67*, *100313*: *76*, *100314*: *70*, *100316*: *79*, *100319*: *56*; *Liang P.H. 86163*: *82*; *Liang T. 4359*: *86*; *Liao A.M. 507*: *52*; *Liao C.J. s.n.*: *27*, *15249*: *86*; *Liao Jih-Ching 10006*: *68*, *10085*: *24*, *10457*: *68*, *& Yien-kuan Lai 10534*: *37*, *10654*: *68*; *Licent Abbé E. 2539*: *48*; *Lin Pi 6488*: *44*; *Lin Q.Z. 10365*: *67*, *10435*: *67*; *Lin Ye Ting 33*: *81*, *920*: *55*; *Ling Le Exped. 32928*: *5*; *Linsley Gressitt J. 350*: *68*; *Liou T.N. 7249*: *44*; *Liu J.C. 368*: *44*, *& C. Wang 85178*: *16*, *& C. Wang 85522*: *38*; *Liu J.H. 89847*: *38a*; *Liu L.F. 5354*: *6*, *5624*: *6*, *5671*: *76*; *Liu L.Y. 15036*: *14*, *15146*: *38a*; *Liu T.S., Liao J.C. & Kuo C.M. 2105*: *50*; *Liu Y.A. 101762*: *70*; *Liu Y.S. 1174*: *46*, *1212*: *46*, *1401*: *14*, *2191*: *45*; *Liu Y.Z. 1*: *82*; *Lo H.S. 28146*: *27*; *Long G.R. 830090*: *74*, *840223*: *82*; *Long Sheng Exped. 130*: *38a*, *144*: *67*, *50180*: *67*, *50403*: *76*, *50416*: *67*; *Long Y.Z. 242*: *44*; *Long Zhou Exped. 274*: *24*; *Lu Q.H. 20*: *24*, *2873*: *38a*, *3338*: *24*, *3526*: *67*, *4114*: *76*, *4338*: *38*, *4359*: *82*; *Ludlow, Sherriff & Hicks 16108*: *42*; *Luo Cheng Exped. 4-1-165*: *24*, *4-1-1509*: *24*; *Luo Z.J. 2573*: *83*.

*Ma W.W. 2388*: *21*; *MacGregor 13*: *44*, *1610*: *30*, *2452*: *25*; *Maingay 19*: *86*, *387*: *44*; *Maire E.E. 0*: *8*, *s.n.*: *45*, *s.n.*: *87*, *s.n.*: *35*, *171*: *26*, *172*: *26*, *175*: *87*, *304*: *35*, *526*: *35*, *819*: *87*, *857*: *87*, *866*: *35*, *1379*: *87*, *1827*: *87*, *1943*: *87*, *2106*: *87*, *2447*: *87* (type), *3779*: *52*, *3794*: *87*; *Makino T. 6494*: *57* (type); *Manders s.n.*: *73* (type); *Mao P.I. 82 58*: *5*, *4253*: *70*, *27216*: *75*, *64222*: *22*; *Maries s.n.*: *52*; *Martin, Leon & E. Bodinier 2066*: *84* (type); *Masamune G. s.n.*: *68*; *Maximowicz s.n.*: *44*, *s.n.*: *29*, *s.n.*: *68* (type), *s.n.*: *68* (type), *s.n.*: *86* (type), *s.n.*: *29*, *s.n.*: *29*, *1882*: *29*; *McClure F.A. s.n.*: *36*, *79*: *36*, *201*: *44*, *281*: *76*, *A 342*: *36*, *582*: *77*, (*LU 18246*) *712*: *70* (type), (*LU 18302*) *768*: *70* (type), (*LU 19761*) *782*: *74*, *1457*: *76*, *1547*: *86*, *1556*: *86*, *2305*: *55*, (*C.C.C. herb. nr.*) *6669*: *76*, (*C.C.C.*) *8593*: *77* (type), (*C.C.C.*) *9652*: *9*, (*1468 in CCC*) *13292*: *74* (type), *13775*: *86*, *13791*: *76*, *20099*: *24* (type), *20124*: *24*, (*CCC herb. nr.*) *952653*: *76*; *McLarens's collectors F 4*: *60*, *L 6 A*: *60*, *UK 8*: *87*, *F 9*: *87*, *AA 13*: *87*, *AD 15*: *35*, *L 18*: *87*, *L 57*: *26*, *F 57*: *87*, *L 66 A*: *35*, *P 82*: *26*, *85*: *42* (type), *C 92*: *35*, *L 101*: *35*, *M 111 A*: *26*, *L 116*: *36*, *M 131*: *26*, *U 170*: *26*, *AA 178*: *26*, *C 180*: *26*, *AA 222*: *14*, *C 228*: *26* (type), *C 246*: *26*; *Mell Pl. Mellianae 721*: *76*; *Menglian Exped. 10145*: *89*;

*Merrill E.D. 10904*: *9*, *11041*: *76*; *Metcalf T.P. 433*: *36*, *1966*: *76*, *17465*: *76*, *17784*: *76*, & *Lau Fun 18247*: *76*; *Meyer F.G. 3335*: *35*, *3354*: *32*, *3357*: *33*, *3364*: *14*, *3368*: *32*, *3399*: *26*; *Meyer F.N. 1504*: *52*, *1572*: *30*; *Miao R.H. 40169*: *86*; *Mombeig, Père 11*: *42*; *Murata G. 18665*: *50*; *Murata J. 10506*: *87*, *10635*: *87*.

*Nan Dan Exped. 4-5-787*: *24*; *Nanzhidi 3719*: *84*, *3768*: *86*, *3806*: *76*, *5310*: *5*; *Nie M.X. 8831*: *82*; *Nong Gang Exped. 10132*: *24*; *North East Yunnan Expedition 754*: *83*.

*Oiu H.X. 0*: *3*; *Oldham R. s.n.*: *25*, *530*: *51*, *977*: *68*.

*Pang C.F. 28*: *1*; *Parmentier s.n.*: *64*; *Pasheng 2*: *77*; *Peal S.E., Herb. LB 908126 709*: *89* (type); *Pei C. 10242*: *46*; *Pen W.M. 12931*: *76*; *Pen Z.H. 51279*: *86a*; *Petelot A. s.n.*: *66*, *s.n.*: *73*, *3379*: *82* (type), *3548*: *81*, *3698*: *60*, *3699*: *82*, *3700*: *84*, *3756*: *66*, *3760*: *14*, *3761*: *60*, *3953*: *70*, *3955*: *70*, *3963*: *6*, *3965*: *70*, *4161*: *22*, *5074*: *40*, *5661*: *81*, *6454*: *64*, *6545*: *59*, *8361*: *59*, *8416*: *14*, *30896*: *40*, *36553*: *14*; *Pierre H.L. s.n.*: *56*, *750*: *89* (type), *752*: *24*; *Poilane 297*: *77*, *1293*: *79*, *1857*: *88* (type), *2063*: *66*, *7092*: *70* (type), *11253*: *75* (type), *12578*: *60*, *12611*: *66* (type), *12864*: *73* (type), *17062*: *40*, *17080*: *40*, *17092*: *6*, *18820*: *60*, *18893*: *81*, *20714*: *7* (type), *20969*: *6*, *21816*: *6*, *22459*: *9b*, *23172*: *77*, *23729*: *60*, *29912*: *24*, *30086*: *79*, *30221*: *14*, *30711*: *40*, *31039*: *38b* (type), *32115*: *70*, *35782*: *40*; *Pratt A.E. 798*: *45*; *Pucha Biaoben 23252*: *48*; *Put 3759*: *60*.

*Qi C.J. 6213*: *38a*; *Qian Bei Exped. 89*: *44*, *869*: *67*, *2250*: *84*; *Qiannan Exped. 1935*: *86*, *2081*: *14*, *3112*: *30*; *Qiao H.R. 1010*: *43*, *1114*: *8*; *Qin H.F. 53*: *81*, *238*: *79*, *70033*: *86*; *Qin, B 5555*: *33*, *66510*: *33*; *Qiu B.Y. 53257*: *14*.

*Read B.E. 1070*: *44*, *R 1071*: *52*; *Rehder, Alfred 737 a*: *48* (type); *Reveal, James L. & James A. Duke 5734*: *87*; *Rock J.F. 1543*: *57*, *2766*: *60*, *3040*: *26*, *3998*: *26*, *6257*: *26*, *6919*: *64* (type), *7739*: *60*, *7888*: *60*, *7933*: *60*, *7961*: *60*, *8015*: *57*, *8620*: *35*, *8639*: *35*, *9625*: *60* (type), *10136*: *38*, *10160*: *31*, *10209*: *32* (type), *10235*: *38*, *10661*: *87*, *11215*: *31*, *11231*: *32*, *11232*: *38*, *11517*: *42*, *11737*: *87*, *11744*: *87*, *17097*: *31*, *18340*: *14*, *18394*: *31*, *21990*: *38*, *21991*: *14*, *22047*: *32*, *22457*: *38*, *22458*: *14*, *22480*: *32*, *22607*: *31*, *22694*: *42*, *23066*: *42* (type), *23284*: *42*.

*Sargent C.S. 0*: *9*; *Sasaki S. s.n.*: *25*, *93*: *68*; *Schneider C. 64*: *87*, *332*: *26*, *362*: *26*, *407*: *26*, *607*: *87*, *2607*: *14*, *4053*: *87*; *Schoch O. 52*: *87*; *Service forestier 0*: *7*, *38204*: *88* (type); *Shi G.L. 14241*: *77*; *Shixi Dui 1957 22*: *60*; *Sin S.S. 9052*: *76*, *9822*: *70*, *9966*: *7*; *Sing I.Y.* (*herb. nr. 18350*) *817*: *77*; *Sino-Amer. Bot. Exped. 330*: *14*, *1181*: *46*, *1338*: *26*, *1413*: *87*, *1630*: *26*; *Sino-American Guizhou Bot. Exped. 154*: *67*, *396*: *67*, *873*: *9*, *1077*: *70*, *1593*: *67*, *1983*: *67*; *Sino-British Exped. 37*: *67*, *K 41*: *87*, *K 152*: *87*, *157*: *42*, *166*: *42*, *655*: *35*; *Sino-Rossica Exped. 17*: *87*, *952*: *14*, *5627*: *89*; *Sino-Rossica Yunnan Exped. 1532*: *57*; *Smith, Harry 1595*: *87*, *1953*: *35*; *Song X.H. 172*: *6*, *244*: *76*, *478*: *76*; *Sonohara S. 82*: *68*; *Soulié J.A. 1576*: *42*; *Steward A.N. c.s. 637*: *67*, *745*: *3*, *748*: *67*, *2001*: *44*, *herb. nr. 2642*: *3*, *4730*: *44*, *11134*: *56*, & *Cheo, H.C. 23*: *67*, & *Cheo, H.C. 452*: *67*, & *Cheo, H.C. 817*: *9b*, & *Cheo, H.C. 849*: *82*, & *Cheo, H.C. 870*: *60*, & *Cheo, H.C. 1078*: *77*, *C.Y. Chiao & Cheo, H.C. 637*: *67*, *C.Y. Chiao & Cheo, H.C. 748*: *67*, *C.Y. Chiao & Cheo, H.C. 764*: *67*, *C.Y. Chiao & Cheo, H.C. 870*: *67*; *259*: *65*, *341*: *21*; *Sun S.C. 1293*: *30*, *1305*: *44* (type); *Susuki Jokio 6098*: *68*; *Susuki S. s.n.*: *68*; *Szechuan University 53909*: *65*, *57205*: *65*, *57258*: *65*.

*Taam Y.W. 19*: *86*, *542*: *86*, *557*: *86*, *572*: *70*, *1276*: *86*, *2149*: *24*; *Tam P.C. 57604*: *88*, *62498*: *70*, *63322*: *14*, *63667*: *76*; *Tang G.G. 679*: *67*; *Tang H.C. 27*: *86*, *s.n.*: *24*, *s.n.*: *24* (type), *461*: *9*, *3703*: *81*; *Tang S.G. 5924*: *86*, *7167*: *86*, *13541*: *86*, *13608*: *86*, *16106*: *86*, *16561*: *86*, *16589*: *86*; *Tang S.I. 634*: *76*; *Tang S.L. 723*: *88*; *Tao D.T. 413*: *54*; *Taquet 167*: *33*; *Tashiro Z. s.n.*: *33*, *s.n.*: *33*; *Ten Simeon 302*: *35*, *500*: *35*, *564*: *35*, *593*: *35*; *Teng H.K. 558*: *87*; *Teng S.M. 339*: *63* (type); *Teng S.W. 90180*: *52*; *Ting K.C. & K.L. Shih 630*: *86*, & *K.L. Shih 1085*: *76*, & *K.L. Shih 1090*: *86*, *etc.*, *1323*: *76*, & *K.L. Shi 1590*: *24*, *etc. 2020*: *76*; *To Kang Peng. s.n.*: *55*, *97*: *86*, *285*: *55*, (*C.C.C.*) *95. 2653*: *55*, (*C.C.C.*) *herb. 2856*: *25*, (*C.C.C.*) *11126*: *55*; *Togashi M. s.n.*: *50*, *529*: *33*; *Touche J. de la 31*: *76*, *134*: *52*; *Tsai H.T. 59- 10917*: *27*, *50843*: *45*, *51702*: *14*, *51745*: *60*, *51802*: *60*, *51831*: *45*, *52805*: *26*, *53006*: *87*, *53053*: *87*, *53143*: *26*, *53355*: *87*, *53380*: *87* (type), *53491*: *87*, *54858*: *38*, *55887*: *57*, *56371*: *60*, *56560*: *14* (type), *56870*: *60*, *56961*: *73* (type), *58573*: *42*, *58698*: *40*, *58995*: *57*, *59903*: *42*, *61619*: *22*, *61621*: *81*; *Tsang H.L. 32980*: *65*, *33747*: *42*, *34828*: *45*; *Tsang W.T.* (*LU 15822*) *323*: *81*, (*LU 17187*) *438*: *81*, (*LU 16203*) *704*: *81*, & *W.K. Chow 2738*: *70* (type), *3044*: *76*, *20119*: *86*, *20291*: *70*, *20440*: *9*, *20992*: *86*, *21066*: *86*, *21134*: *86*, *22074*: *24*, *22185*: *24*, *22630*: *70*, *22753*: *82* (type), *22769*: *70*, *24422*: *70*, *24463*: *38b*, *24876*: *76*, *24947*: *76*, *24957*: *86*, *25099*: *86*, *25175*: *19*, *25627*: *74*, *25847*: *86*, *26118*: *76*, *26118*: *76*, *26656*: *24*, *26813*: *6*, *26866*: *81*, *26868*: *81*, *27391*: *70*, *28495*: *30*, *28559*: *82*, *28700*: *86*, *29007*: *24*, *29316*: *6*, *29437*: *24*, *29957*: *6*, *31138*: *76*; *Tsang & Fung 656*: *9* (type), *538* (*L.U. 18072*): *24* (type), *LU 18190*: *9* (type); *Tse H. 137*: *86*, *662*: *70*, *695*: *7*; *Tsiang T. 12059*: *75*, *12089*: *75*; *Tsiang Y. 39*: *86*, *485*: *56*, *521*: *76*, *821*: *86*, *1048*: *36*, *1281*: *14*, *1757*: *25*, *2609*: *74* (type), *2802*: *36*, *2889*: *76*, *4141*: *67*, *5361*: *52*, *6801*: *52*, *6933*: *76*, *6984*: *76*, *7534*: *67*, *7589*: *60*, *7859*: *67*, *7906*: *67*, *8543*: *52*, *8671*: *84*, *9169*: *30*, *10012*: *86*, *10411*: *52*, *10616*: *30*, *10701*: *44*, *10703*: *3*, *11285*: *87*, *13022*: *87*, *13430*: *57*, & *H. Wang 16023*: *26*, & *H. Wang 16025*: *87*, *Tso C.L. 20354*: *70*, *20508*: *7*, *20561*: *70*, *20569*: *76*, *20671*: *25*, *20905*: *7*, *20984*: *76*, *21005*: *9*, *21033*: *82* (type), *21098*: *7*, *21173*: *7*, *23510*: *81*, *43749*: *81*; *Tsoong C.H 82048*: *67*, *81657*: *14*, *81948*: *9*, *82074*: *33*, *83515*: *33*, *83580*: *6*, *83704*: *76*, *84761*: *6*, *90960*: *76*, *808128*: *36*, *808954*: *67*, *808958*: *82*, *809507*: *74*, *809507*: *77*; *Tsui T.M. 90*: *86*; *Tu & Sun 4070*: *3*; *Tutcher W.T. 637*: *86*.

*Uchiyama T. 4065*: *33*; *Ueda K. 459*: *33* (type).

*Vidal J.E. 653 A*: *70*, *1629*: *14*, *4932*: *14*.

*Wai Chung Ping 13791*: *76*; *Walker E.H. c.s. 6640*: *68*; *Wallich s.n.*: *14* (type), *s.n.*: *64* (type), *s.n.*: *62*, *s.n. 970*: *57*, *970 A*: *62*, *973*: *14* (type), *6493*: *64*, *6494*: *57* (type); *Wang C. 2888*: *77*, *30003*: *76*, *31135*: *9*, *et al. 31305*: *86*, *31404*: *76*, *32199*: *70*, *33359*: *24*, *33629*: *81*, *34512*: *9*, *35367*: *77*, *35992*: *77*, *36050*: *9*, *36233*: *77*, *39230*: *9*, *39396*: *6*,

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- ☐ Text is in English or Spanish on numbered pages.
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- ☐ A one-paragraph abstract precedes text. Papers in Spanish have an English abstract in addition to a Spanish resumen.
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## Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 1992

| | 1992 | | |
|---|---|---|---|
| | Vascular | Bryophyte | Total |
| Acquisition of specimens | | | |
| Staff Collections (includes bryophytes) | 62,547 | — | 62,547 |
| Purchase | 2,157 | 535 | 2,692 |
| Exchange | 50,141 | 2,380 | 52,521 |
| Gifts | 12,503 | 1,671 | 14,174 |
| Total acquisitions | 127,348 | 4,586 | 131,934 |
| Mountings | | | |
| Newly mounted | 169,289 | 16,100 | 185,389 |
| Mounted when received | 1,633 | 0 | 1,633 |
| Total specimens filed | 170,922 | 16,100 | 187,022 |
| Repairs | | | |
| Specimens repaired | 21,227 | | 21,227 |
| Specimens stamped | 2,728 | | 2,728 |
| Total repairs | 23,955 | | 23,955 |
| Specimens sent | | | |
| On exchange | 51,906 | 5,266 | 57,172 |
| As gifts | 13,277 | 799 | 14,076 |
| Total | 65,183 | 6,065 | 71,248 |
| Loans sent | | | |
| Total transactions | 427 | 39 | 466 |
| Total specimens | 27,943 | 4,251 | 32,194 |
| To U.S. institutions | | | |
| Transactions | 231 | 23 | 254 |
| Specimens | 14,612 | 378 | 14,990 |
| To foreign institutions | | | |
| Transactions | 196 | 16 | 212 |
| Specimens | 13,331 | 3,873 | 17,204 |
| To student investigators | | | |
| Transactions | 51 | 3 | 54 |
| Specimens | 6,823 | 37 | 6,860 |
| To professional investigators | | | |
| Transactions | 376 | 36 | 412 |
| Specimens | 22,734 | 2,600 | 25,334 |
| Loans received | | | |
| Transactions | 355 | 17 | 372 |
| Specimens | 20,485 | 2,119 | 22,604 |

| | 1992 | | |
|---|---|---|---|
| | From U.S. | From abroad | Total |
| Visitors | 409 | 126 | 535 |

On 31 December 1992 the total number of mounted, accessioned specimens in the herbarium was 4,112,057 (3,892,146 vascular plants and 219,911 bryophytes).

## Recent Issues of the *Annals of the Missouri Botanical Garden*

### Phylogeny of Asteridae

*Annals of the Missouri Botanical Garden* 79(2) (Spring 1992). The monophyly, sister group (or groups), and patterns of relationships of the Asteridae are discussed in the symposium "Phylogeny of Asteridae," organized by Larry Hufford of the University of Minnesota. The symposium was jointly sponsored by the American Society of Plant Taxonomists and the Botanical Society of America and was held at their annual meeting, 7 Aug. 1990, in Richmond, Virginia. 238 pages. $27.00, plus postage.

### Knowledge Brokering: The Mechanics of Synthesis

*Annals of the Missouri Botanical Garden* 80(2) (Spring 1993). This symposium, the 38th Annual Systematics Symposium of the Missouri Botanical Garden (held 4–5 Oct. 1991, in St. Louis, Missouri), discusses the value and future necessity of assimilating diverse biological information into new and broader syntheses, taking advantage of computer-based data-management systems. 41 pages (entire issue 230 pages). $35.00, plus postage.

### *rbc*L Sequence Data and Phylogenetic Reconstruction in Seed Plants

*Annals of the Missouri Botanical Garden* 80(3) (Summer 1993). Fourteen papers plus an appendix containing voucher and sequence data. This collection of papers, organized by Douglas E. Soltis and Mark W. Chase, presents the first in-depth molecular phylogenetic analysis of seed plants in general, and angiosperms in particular. Investigators throughout the world involved in *rbc*L sequencing studies contributed their unpublished sequences for a broad phylogenetic analysis. 235 pages. $40.00, plus postage.

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**Cover illustration.** *Pleurothyrium giganthum* van der Werff, by J. Myers.